

Tracking of Black-legged Kittiwakes from an offshore platform in the Dutch North Sea during summer

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Abstract

Black-legged Kittiwakes *Rissa tridactyla* (hereafter 'Kittiwakes') have increasingly been breeding on anthropogenic structures, including offshore platforms. Breeding on offshore platforms may result in smaller foraging ranges compared to natural breeding sites due to closer proximity to feeding areas and/or reduced competition at sea in comparison to mainland, coastal colonies of the same size, due to the greater access to sea area. We GPS-tracked nine Kittiwakes breeding on an offshore platform in the Dutch North Sea and compared movements between estimated breeding stages. Focusing on the early chick-rearing period, analysis of foraging ranges found in literature suggested shorter foraging ranges in colonies with greater access to sea area, and that foraging ranges of Kittiwakes breeding on platform L7-B were shorter than expected for a similarly sized coastal colony. Maximum trip distance increased during the estimated late chick-rearing and post-fledging periods and decreased again from mid-August to late September (post-breeding) with more time spent in the colony after which the birds did not return to the platform. During the entire study period, but most frequently in September, Kittiwakes visited one to seven other platforms, including platforms previously documented to host breeding Kittiwakes, suggesting prospecting behaviour. Remaining major knowledge gaps are the number of Kittiwakes breeding on platforms in the (Dutch) North Sea and their role in the meta-population dynamics of the North Sea population.

Introduction

The Black-legged Kittiwake *Rissa tridactyla* (hereafter 'Kittiwake') is a small pelagic gull with a circumpolar distribution that has shown marked population declines over the past decades in most of its distribution (Keller *et al.* 2020). Following these declines, the species is classified as *Vulnerable* on the Global (BirdLife International 2019) and *Endangered* on the European Red List of threatened species (BirdLife International 2021). Within Europe, there are some regional differences: the species is classified as *Vulnerable* in Iceland (IINH 2018), *Endangered* in Norway and the United Kingdom (Stanbury *et al.* 2021; Stokke *et al.* 2021), and in The Netherlands it is classified as *Near-threatened* based on the small population size and distribution (Kleunen *et al.* 2017). The population decline of Kittiwakes appears mainly driven by climate change, where increased sea surface temperatures result in reduced breeding productivity and reduced non-breeding survival (Reiertsen *et al.* 2014; Sandvik *et al.* 2014; Descamps *et al.* 2017; Frederiksen *et al.* 2023). In addition, Kittiwake populations can be negatively affected by competition with fisheries (Frederiksen *et al.* 2004) and predation (Anker-Nilssen *et al.* 2023).

Kittiwakes usually breed on coastal cliffs, but the species has over the last decades increasingly occupied anthropogenic structures. These include buildings and bridges in coastal towns, but also offshore oil and

gas platforms (Camphuysen & De Vreeze 2005; Christensen-Dalsgaard *et al.* 2019). Breeding at offshore platforms potentially has several advantages over coastal sites. Offshore platforms may be in closer proximity to foraging areas, requiring shorter foraging trips, which has several benefits that increase breeding success. Besides the location of key foraging grounds to the colony and the general availability of food (Suryan *et al.* 2000), foraging ranges of Kittiwakes and other seabirds generally increase with colony size (Jovani *et al.* 2016; Patterson *et al.* 2022; Cleasby *et al.* 2023), which is attributed to depletion or antipredator behaviour of prey close to the colony (Ashmole 1963; Hemerik *et al.* 2014). Local prey depletion is expected to be less when birds have greater access to sea area closer to the colony, as is the case when breeding on a platform or island from where birds can venture in all directions, as opposed to coastal sites where part of the area surrounding colonies is occupied by land (Jovani *et al.* 2016; Wakefield *et al.* 2017). Therefore, Kittiwakes breeding on offshore platforms might benefit from lower intra-specific competition resulting in smaller foraging ranges. Breeding on offshore platforms is also likely to result in lower predation pressure, as predators such as White-tailed Eagles *Haliaeetus albicilla* and corvids will not or only rarely occur far offshore (Christensen-Dalsgaard *et al.* 2019; Anker-Nilssen *et al.* 2023). Indeed, productivity of Kittiwakes breeding at offshore oil rigs appears higher than on natural breeding ledges in Norway (Christensen-Dalsgaard *et al.* 2019).

In the Netherlands, where there is no natural breeding habitat for Kittiwakes and no nesting occurs in coastal towns, Kittiwakes were first reported to breed on offshore platform L8-P in 2000 (Camphuysen & De Vreeze 2005). Breeding Kittiwakes have since been found breeding on three other platforms in Dutch waters, with several additional platforms where potentially prospecting adults were observed (Camphuysen & Leopold 2007; Geelhoed *et al.* 2011; Fijn *et al.* 2023). Information on the number of breeding pairs and occupancy of platforms has remained anecdotal due to limited access to the platforms: most records stem from observations from ships during ship-based seabird surveys. Only in 2005 and 2023 could colonies at platforms be visited to collect additional data on, e.g. clutch and egg sizes and diet (Camphuysen & De Vreeze 2005; Fijn *et al.* 2023). Hence, virtually nothing is known on the productivity and ecology of Kittiwakes breeding in the Netherlands. Counts are available for multiple years for only two platform colonies: L8-P and L7-B. The colony at L8-P grew from three nests in 2000-2001 to 45 pairs in 2005 (Camphuysen and De Vreeze 2005) and then decreased to 32 nests in 2006, presumably after removal of nests early in the season following concerns of Highly Pathogenic Avian Influenza (Camphuysen & Leopold 2007). Since its discovery, the colony at L7-B increased, with four nests in 2006 (Camphuysen & Leopold 2007), nine nests in 2016 (Geelhoed & Leopold 2016), 13 nests in 2019 (Geelhoed *et al.* 2019) and *ca.* 200 breeding pairs in 2021. The L7-B platform could be surveyed as part of our study, resulting in 350-400 Apparently Occupied Nests (AON) in 2023 (Fijn *et al.* 2023). Following the count at L7-B, the Dutch breeding population has been updated from 50-150 breeding pairs in 2013-15 (Geelhoed 2019) to >350 breeding pairs (www.sovon.nl, accessed 16 July 2024). However, with no recent information from platforms other than L7-B, this is likely an underestimate, which is supported by the 10,000s (with wide confidence intervals) of Kittiwakes that were estimated to be present in the Dutch sector of the North Sea based on aerial seabird surveys in June 2018-2023 (van Bemmelen *et al.* 2023). Higher densities of Kittiwakes observed during these surveys cluster where most platforms with breeding Kittiwakes in Dutch waters are located, suggesting that this may be in part attributable to birds breeding on these platforms. Knowledge of foraging ranges of platform-breeding Kittiwakes may help in understanding the abundance estimates and distributions obtained from aerial surveys.

Here, we studied the movements of individual Kittiwakes breeding on the L7-B offshore platform on the Dutch Continental Shelf, using GPS-loggers. Specifically, we were interested in where they foraged, in which directions from the platform, and the duration and maximum distance of their foraging trips.

Considering they should be able to venture in all directions from the platform, we expect lower competition directly surrounding the colony in comparison to a coastal breeding site. Therefore, we hypothesised that they forage closer to the colony than predicted for coastal colonies of similar size, based on the typical foraging ranges observed across both coastal and island Kittiwake colonies tracked in earlier studies. To focus future survey effort, we were also interested in which other platforms were visited by the tracked Kittiwakes, considering that they may prospect other colonies or potential breeding habitat (Boulinier *et al.* 1996).

Methods

Study site

Breeding Kittiwakes were studied at the gas platform L7-B (53.60°N, 4.20°E; Figure 1), in the Dutch sector of the North Sea, sited at a water depth of 34 m. This platform was operational from 1977 to 2017 but has since been out of production and unmanned. During the fieldwork, the colony size was estimated at 350-400 breeding pairs (Fijn *et al.* 2023).

GPS-tracking

On 6 June 2023, breeding adults were captured on the nest using a noose on a 4 m pole. Birds were fitted with a metal ring, a colour ring and Ecotone GPS-loggers (model PICA, 36x17x12 mm) using leg-loops (N = 8) or full body (N = 2) harnesses, constructed from 2 mm wide Teflon. The total weight of the logger, Teflon and rings was 6 g. With an average body mass of 362 ± 28 g (range: 316–397 g), the added weight represented 1.6% (range: 1.5–1.9%) of the body weight. To balance battery life and resolution of the data, loggers were set to record positions each 15 minutes from 6:00 to 18:00 UTC. When the battery voltage dropped below 3.7 V, loggers switched to taking one position per hour. A base station placed on the platform registered when loggers were within c. 400 m, upon which loggers transferred data to the base station. Birds were sexed based on biometrics using Coulson (2009), which indicated that our sample included four males and six females. Sex is indicated in figure labels for individuals as F (female) and M (male).

Delineating breeding stages

As we did not have direct observations of breeding stage of the tracked birds, we defined breeding stages across all tracked individuals. We inferred that eggs likely hatched around 11 June, based on the observation of a sudden drop in maximum trip distances after hatching, which has also been reported in literature (Robertson *et al.* 2014). Subsequent breeding stages were delineated from this estimated hatching date, assuming that chicks fledged at an age of 42 days and returned to the colony up to 61 days after hatching (Coulson 2011, and references therein). Considering most earlier tracking studies concern data from the early chick-rearing period only, we divided the chick-rearing period into an early (first 21 days) and late period. Based on these criteria, we defined the incubation period as the time from catching to 11 June, the early chick-rearing period from 12 June to 2 July, the late chick-rearing period from 3 July to 23 July, the post-fledging period from 24 July to 11 August and the post-breeding period from 12 August to the end of the tracking data on 23 September.

Movements of Kittiwakes breeding on an offshore platform

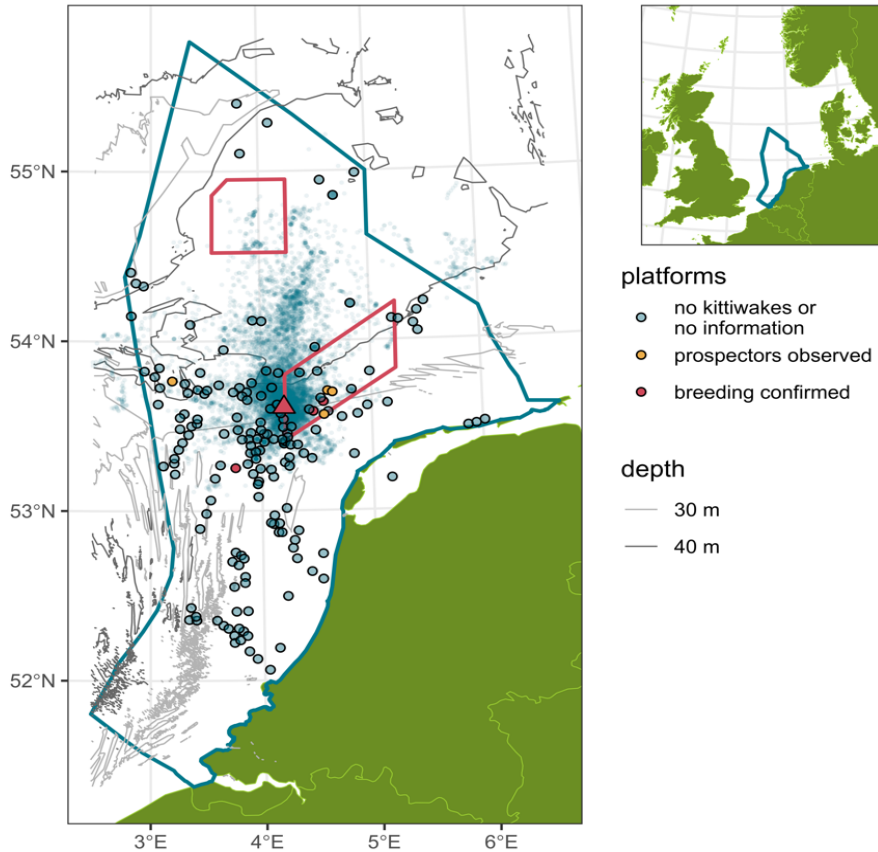


Figure 1. The Dutch sector of the North Sea (blue line), showing the distribution of platforms (filled dots) and the GPS tracking data of nine Black-legged Kittiwakes *Rissa tridactyla* (transparent blue dots). The colony platform L7-B is shown as a red triangle. Red dots indicate other platforms where breeding Kittiwakes have been reported and orange dots show platforms with potentially prospecting adults, based on Camphuysen & Leopold (2007) and Geelhoed et al. (2011). Grey lines show depth isolines of 30m (light grey lines) and 40m (dark grey lines). The two areas outlined in red are the Central Oystergrounds as assigned under the marine framework directive in the north and the Natura 2000 area the Frisian Front just east of the breeding platform L7-B. The inset shows the Dutch sector within the wider North Sea.

Foraging trips

Following Cleasby *et al.* (2023), foraging trips were defined as uninterrupted periods of tracking data further than 1 km from the colony centre. This excludes birds that rest on the platform or at sea in proximity to the platform. For each trip, we calculated the duration and the maximum Haversine distance from the colony. For each position, the proximity to the closest offshore platform was determined. Birds were assumed to be on the platform when this distance was less than 25 m.

Maximum trip distance

One of our main aims was to test whether 1) access to sea affects foraging ranges of Kittiwakes and 2) whether the foraging ranges of Kittiwakes breeding at L7-B are smaller than what would be expected for a similarly sized coastal colony with less access to sea. Therefore, we collated mean maximum trip distances reported in literature (N = 15, data from Ainley *et al.* 2003; Hamer *et al.* 1993; Humphreys *et*

al. 2006; Kotzerka *et al.* 2010; Chivers *et al.* 2012; Paredes *et al.* 2014; Ostrand *et al.* 1998; Christensen-Dalsgaard *et al.* 2018; Suryan *et al.* 2000; Osborne *et al.* 2020) as well as the colony-level mean posterior estimates from Cleasby *et al.* 2023 (N = 20). These studies and estimates concerned the early chick-rearing phase - with a few exceptions where a small part of the incubation period was included. The study by Cleasby *et al.* (2023) provided a large number of estimates and was based on 602 individual Kittiwakes, tracked for 1–6 days during the late incubation and early chick-rearing period in 1-6 years, from 20 colonies around the UK of which 11 were located along the North Sea coast. For each colony, we computed p_{land} : the percentage of total area made up by land within a distance of 25 km. We chose this distance considering most of the foraging ranges were within that distance and hypothesised that the main effect of land coverage would be apparent close to the colony. Then, we fitted a Bayesian Generalized Linear Mixed Models (GLMMs) with mean maximum trip distance as response, random intercepts for colonies, and p_{land} and \log_{10} colony size as fixed effect. We compared this model to two models with additional fixed effects: 1) p_{land} and 2) the interaction between p_{land} and \log_{10} colony size. Models were fitted using the 'brms' package in R (Bürkner 2017), assuming a gamma distribution, using the log link function and the default uninformative priors. Marginal estimates were obtained using the 'brmsmargins' package (Wiley & Hedeker 2022). We compared the expected log pointwise predictive density (ELPD) of the models using Pareto smoothed importance sampling in Leave-One-Out cross validation (PSIS-LOO-CV), as implemented in the 'loo' package in R (Vehtari *et al.* 2024).

Behavioural states

Periods when the birds were stationary, foraging or in transit were identified using a Hidden Markov Model (HMM), where behavioural states were inferred from two observed variables: step length and turning angle. HMMs were fitted using the 'hmmTMB' package in R (Michelot 2023) and behavioural states were predicted for the original data using the Viterbi algorithm. Random intercepts were included for individuals in the transition and stationary probabilities. Only GPS data with 15-minute intervals between positions were used.

Proportion of time spent in 1) the colony, 2) foraging, 3) in transit, and 4) stationary but outside the colony, were analysed using four beta GLMMs with random intercepts for individuals, using the proportion of 15-minute positions per day in each behaviour as response variable. We used daily proportions instead of the regularised data, to avoid problems with short-term temporal autocorrelation. During a large part of the early chick-rearing period, the base station was low in battery and therefore less often registered loggers as 'in range'. Hence, the positions classified as 'in colony' in this period are largely based on the GPS-positions. The base station likely records birds in the colony with greater accuracy than the GPS-loggers, given the regular failure to take positions by the latter and the short time intervals with which the base station attempts to locate loggers. Therefore, we assumed that presence in colony was recorded with no error by the base station or as GPS-positions within 1 km from the colony as recorded by the GPS-loggers. To estimate the time in colony, we calculated per day the percentage in-colony positions of all 15-minute intervals between 06:00–18:00, irrespective of whether there was GPS-data. The daily proportion of time spent foraging, in transit or stationary was calculated from positions not in the colony and multiplied by the daily proportion of positions not in colony to arrive at total time budgets despite missing data. All analyses were performed in R version 4.4.2 (R Core Team 2023).

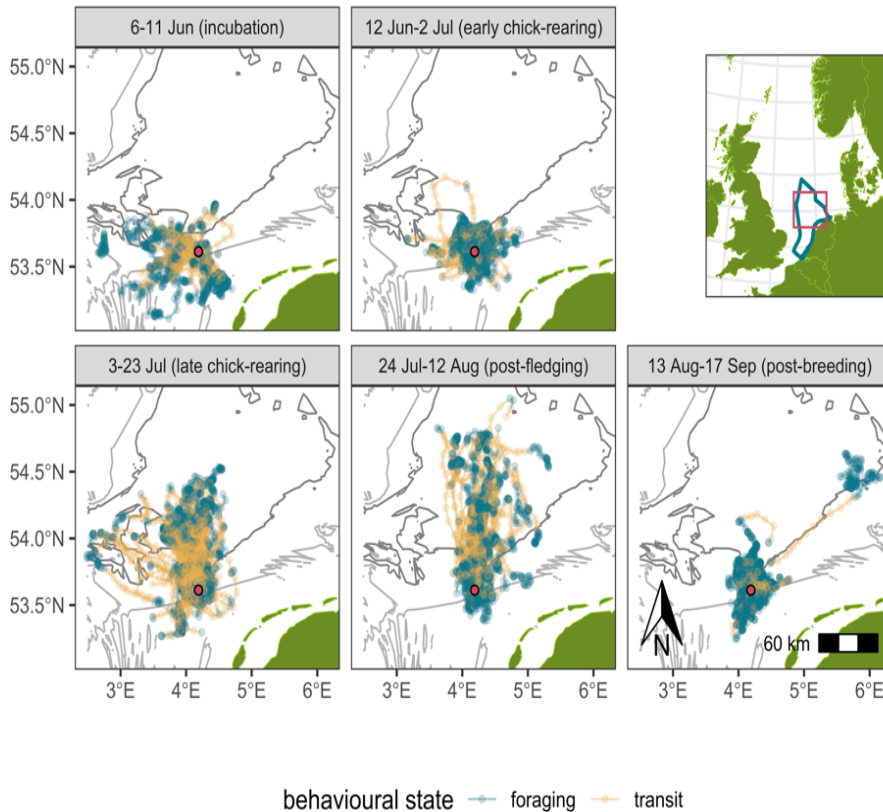


Figure 2. Distribution of positions of nine Black-legged Kittiwakes *Rissa tridactyla* tracked from L7-B (red dot) per assumed breeding stage. Tracks are annotated with two behavioural states. From the positions classified as stationary, 91% were on the L7-B platform and are not discernible here. Grey lines show the -30 m (dark grey) and -40 m (light grey) isobaths; the northern part of The Netherlands (green) is visible in the lower right corners. The red rectangle in the inset map shows the area within the North Sea shown in the subplots.

Results

Of the ten GPS loggers, one produced only five positions in the hour after tagging and was probably lost (Kittiwake ID HOL17). This bird was excluded from analyses below. The remaining nine loggers produced 4,891 to 10,233 positions over a period of 45 to 105 days before the birds left the platform and remained out of reach of the base station until the data was downloaded on 27 October 2023. The first Kittiwake to leave the platform was HOL15, with a last record on 7 August, whereas other birds were recorded up to 4–23 September (median 17 September) (Table A1; Figure A1, see online Supplementary Materials).

Trip characteristics

Overall, mean duration of trips was 2.78 hours (h) (S.D. = 2.8 h, range = 0.03–12.23 h) and the mean maximum distance from the colony was 22.6 km (S.D. = 25.6 km, range = 1–166.3 km, N = 1,092 trips). All but one individual made at least one trip with a maximum distance of c. 100 km or more; the remaining individual ventured up to 78 km from the colony. Variation in maximum trip distance was much more pronounced between periods (Figure 2, 3a) than between individuals (Figure A2a, see online Supplementary Materials). During all periods (Figure 3b) and in all individuals (Figure A2b, see online

Supplementary Materials), trips ventured in all directions, but longer trips were predominantly northwards.

Trips with a maximum distance further than 25 km from the colony occurred predominantly during incubation (67.1% of the trips; N = 85), late chick-rearing (43.9%; N = 271) and post-fledging period (43.1%; N = 144), but formed the minority during the early chick-rearing (9.8%; N = 338) and the post-breeding period (9.1%; N = 254) (Figure 2, 3a).

Maximum trip distances varied substantially between breeding stages (Figure 4, Table A2, see online Supplementary Materials). Substantial differences were apparent between sets of subsequent stages: incubation vs. early chick-rearing ($\beta_{M3-2} - \beta_{M3-1} = -21.9$, 95% CrI = -31.8--15.2, $P < 0.001$); early vs. late chick-rearing ($\beta_{M3-3} - \beta_{M3-2} = 15.8$, 95% CrI = 11.6--21.3, $P < 0.001$), late chick-rearing vs. post-fledging ($\beta_{M3-4} - \beta_{M3-3} = 9.2$, 95% CrI = 2.9--17, $P = 0.001$) and post-fledging vs. post-breeding ($\beta_{M3-5} - \beta_{M3-4} = -28.8$, 95% CrI = -38.8--21.8, $P < 0.001$). In addition, maximum trip distances were even shorter during the post-breeding period than during the early chick-rearing period ($\beta_{M3-5} - \beta_{M3-4} = -3.7$, 95% CrI = -5.9--1.6, $P < 0.001$).

Behavioural states

In the three-state HMM, the 'stationary' state was characterized by short steps (mean = 35 m in 15 min, S.D. = 32 m) and low directionality (mean = -3, kappa = 0), the 'foraging' state had intermediate steps lengths (mean = 1,938 m, S.D. = 1,908 m) and directionality (mean = 0, kappa = 1), whereas the 'transit' state had large steps lengths (7,531 m, S.D. = 2,856 m) and strong directionality (mean = 0, kappa = 9) (Figure A3, see online Supplementary Materials).

During incubation, the tracked Kittiwakes spent on average 44% of their time in the colony. The time in the colony significantly increased to 62% during the early chick-rearing period ($\beta = 17\%$, 95% CrI = 9--25%). This decreased again during subsequent stages to 45%, 40% and 49%, levels similar to the incubation period (Figure 6). The time spent foraging decreased from 39% incubation to 31% during early-chick rearing, after which it increased up to 42 during the post-breeding period. The proportion of time spent in transit varied between 7 and 20% and mirrored maximum trip distances, with lowest proportions during early chick-rearing and post-breeding when birds made only short foraging trips. The proportion of time that birds were stationary outside the colony was generally small and varied between 1 and 3%, being slightly but significantly higher during post-breeding than earlier periods ($\beta = 0.015$, 95% CrI = 0.001--0.031). These patterns varied little between individuals (Figure A4, see online Supplementary Materials).

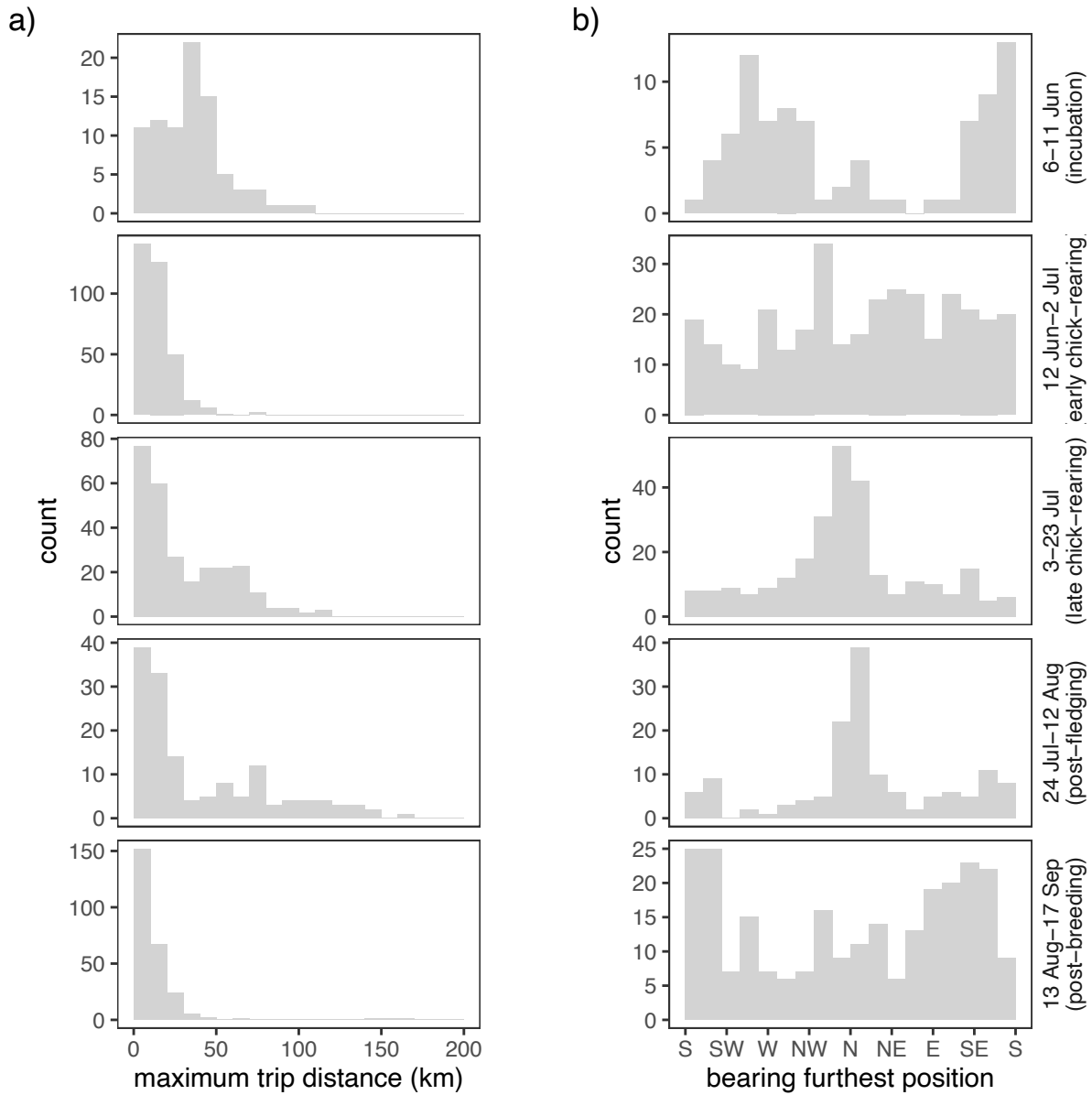


Figure 3. Distribution of a) maximum trip distance and b) direction of trips per breeding stage, for all nine GPS-tracked Black-legged Kittiwakes *Rissa tridactyla* combined.

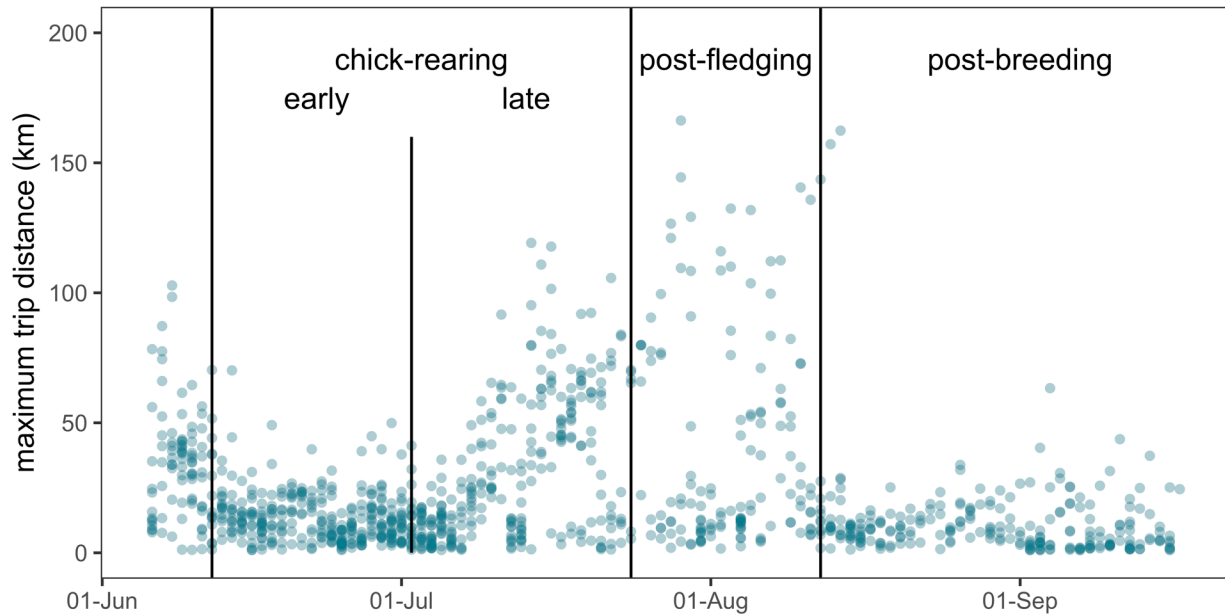


Figure 4. Maximum trip distances of Black-legged Kittiwakes *Rissa tridactyla* breeding at L7-B varied substantially across the study period and between estimated breeding stages.

Colony-level estimates of mean maximum trip distance gleaned from literature showed an increase with \log_{10} colony size (Figure 5). For most colonies, p_{land} was between 0 and 0.5, with peaks at 0.1 and 0.4; a single colony had a p_{land} of 0.8. Among the three GLMMs of colony-level mean maximum trip distance as a function of \log_{10} colony distance and p_{land} , the model with both fixed effects but no interaction performed marginally better than the other two models, with $ELPD_{diff}$ of -0.5 for the model with interaction, and -1.2 for the model without p_{land} . The standard errors of these $ELPD_{diff}$ were 1 and 0.4, respectively, indicating substantial differences in ELPD between these models and the model with the highest ELPD. The posterior for a colony of 375 breeding pairs and a p_{land} of 0.5 was considerably higher ($\mu = 25.3$, 95% CrI = 18.7–34.8) than the posterior of L7-B ($\beta_{lit} - \beta_{L7B} = 10.3$ 95% CrI = 2.9–20.2, $P = 0.004$).

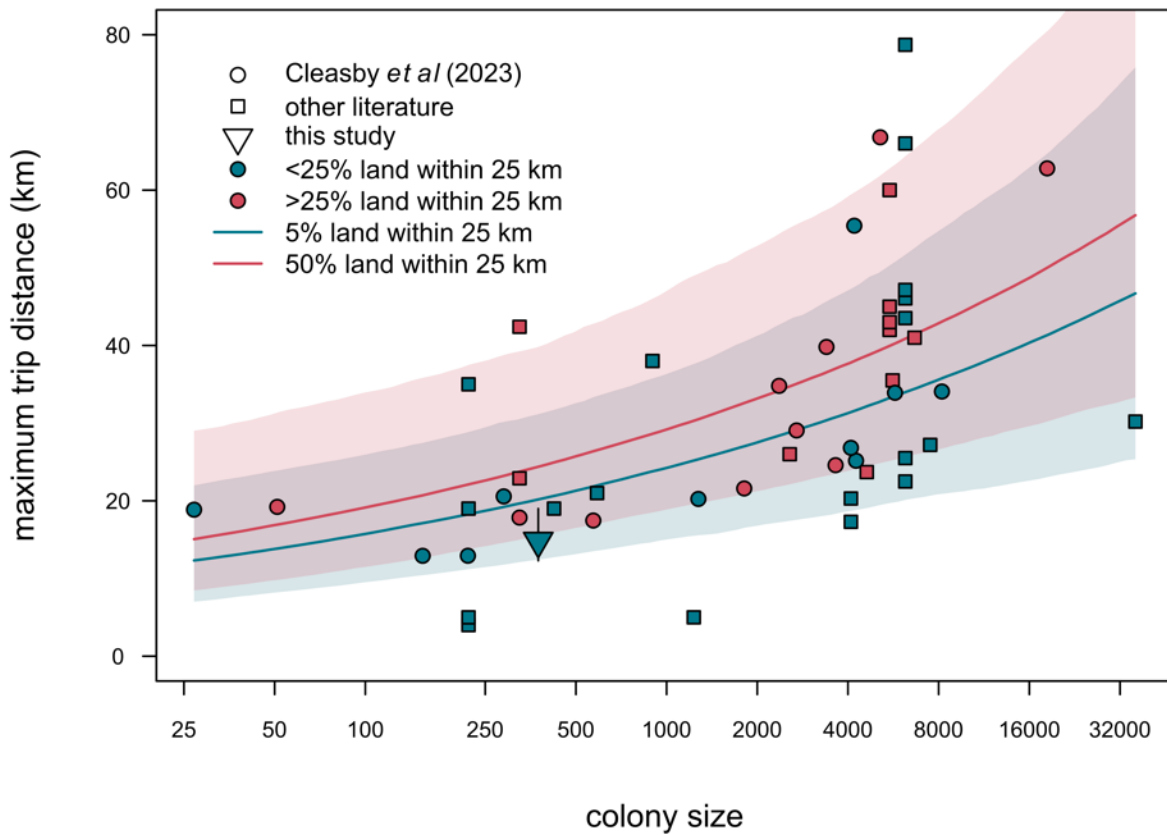


Figure 5. Comparison of Black-legged Kittiwake *Rissa tridactyla* maximum trip distance from our study (inverted red triangle) with conditional model estimates for chick-rearing adults from Cleasby *et al.* (2023) (dots) and other values obtained from literature (squares), showing the effect of colony size and percentage of land within 25 km from the colony. The blue and red lines with associated 95% credible intervals show conditional effects for colonies with 5% and 50% land within 25 km from the colony. Colony size was log₁₀ transformed.

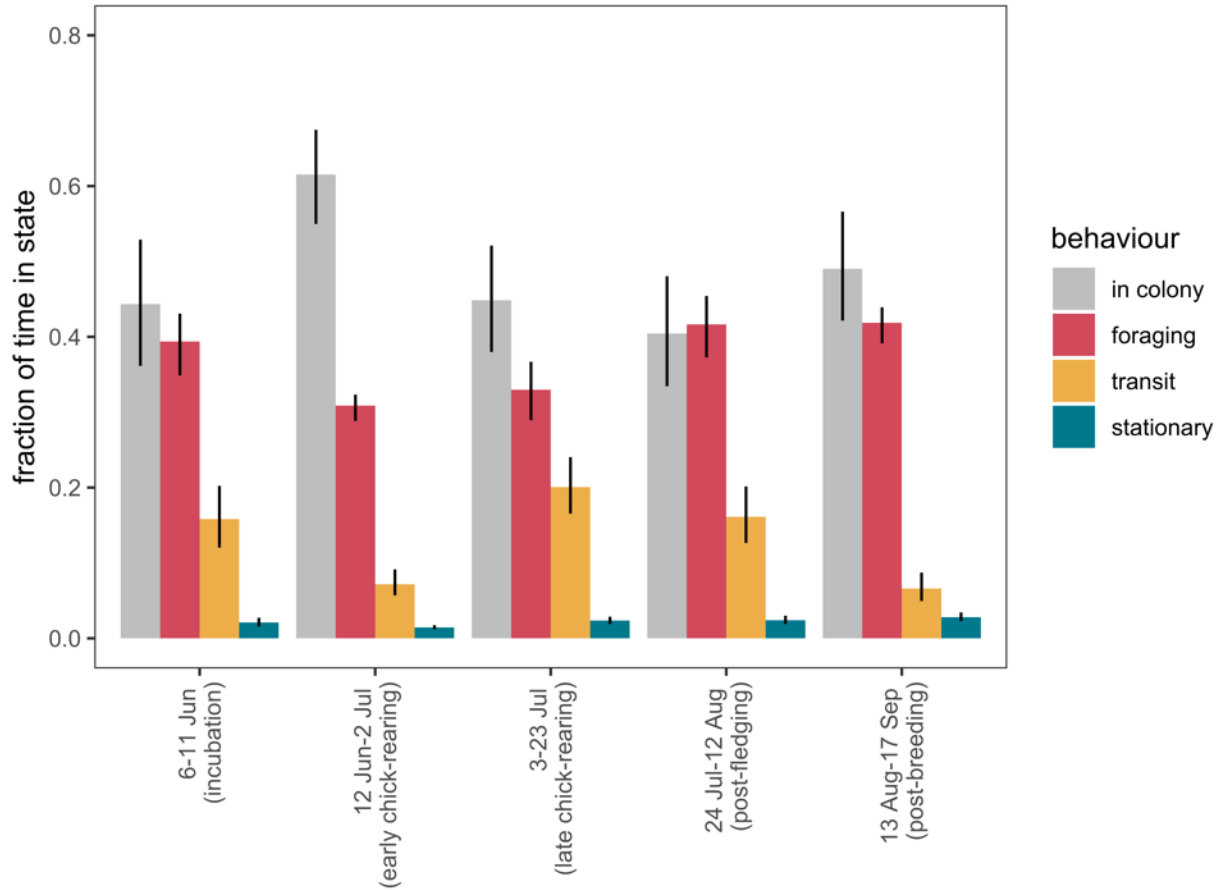


Figure 6. Fraction of time during the day (06:00-18:00, UTC) spent in the colony (grey) or outside the colony in each of three behavioural states of nine GPS-tracked Black-legged Kittiwakes *Rissa tridactyla* breeding on L7-B. Error bars show posterior 95% credible intervals.

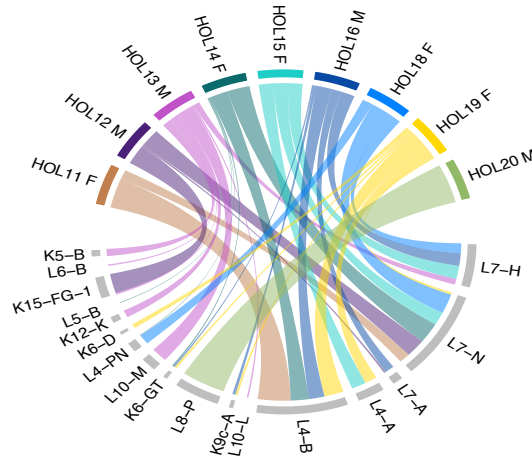
Visits to other platforms

The nine GPS-tracked Kittiwakes visited between one and seven offshore platforms other than the breeding platform (Figure 7a). Visited platforms were located broadly in all directions from the breeding platform (Figure 7b) and at distances of up to 53 km (Figure 8). Some platforms were visited only by a single individual and for short times. Other platforms however, most notably L7-H, L7-N and L4-B, which are all abandoned and thus unmanned platforms (T. Kabel *in litt.*), were visited by multiple individuals and for longer periods (Figure 7a). L7-H and L7-N are respectively 4.51 and 4.61 km from the L7-B breeding platform, whereas L4-B is 15.5 km from L7-B (Figure 7b, 8a). Platforms K5-B, K6-D, K6-GT, L4-A and L4-PN are also unmanned (T. Kabel *in litt.*), but we have no information on the status of other visited and non-visited platforms.

Visits to platforms other than the breeding platform occurred throughout the time that birds were tracked and peaked in September (Figure 8b). When visiting platforms, birds stayed there on average 0.84 h per day, ranging from 15 min (1 GPS-position) to 3.5 h (14 GPS-positions). Visits exceeding 15 min tended to occur more often around mid-August and in September (Figure 8b). Visits were distributed evenly across the daylight hours when GPS-devices were recording.

Movements of Kittiwakes breeding on an offshore platform

a)



b)

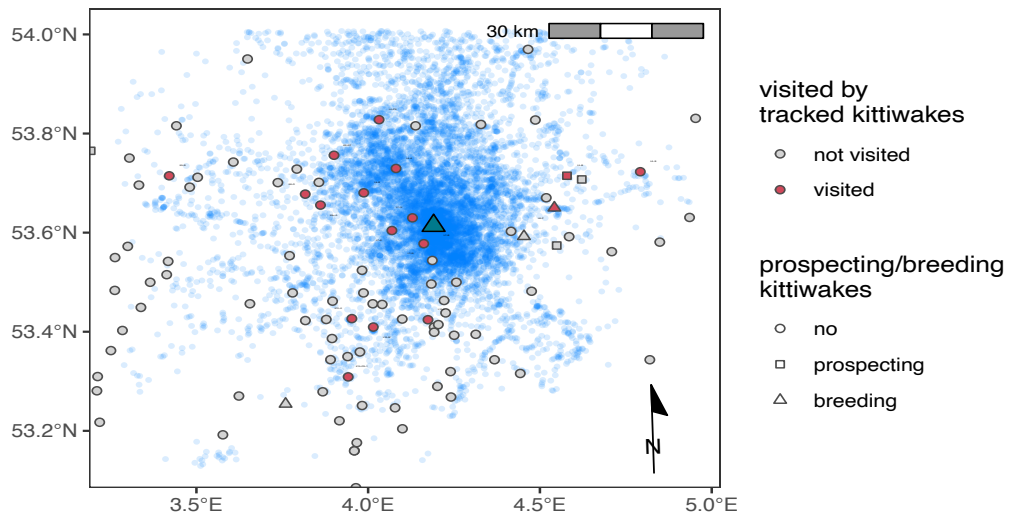


Figure 7. a) Usage of other offshore platforms than L7-B by nine GPS-tracked Black-legged Kittiwakes *Rissa tridactyla* (codes starting with ‘HOL’). M and F represent males and females, respectively. Platforms (L7-H to K5-B) are ordered from farthest (K5-B) to nearest (L7-H) to the colony platform. b) Map of platforms visited (red) and not visited (grey), GPS-positions (pale blue background dots), and L7-B (blue triangle), zoomed to the extent of used platforms to allow details to be visible. Platforms where prospecting or breeding Kittiwakes were reported in earlier publications are shown as triangles.

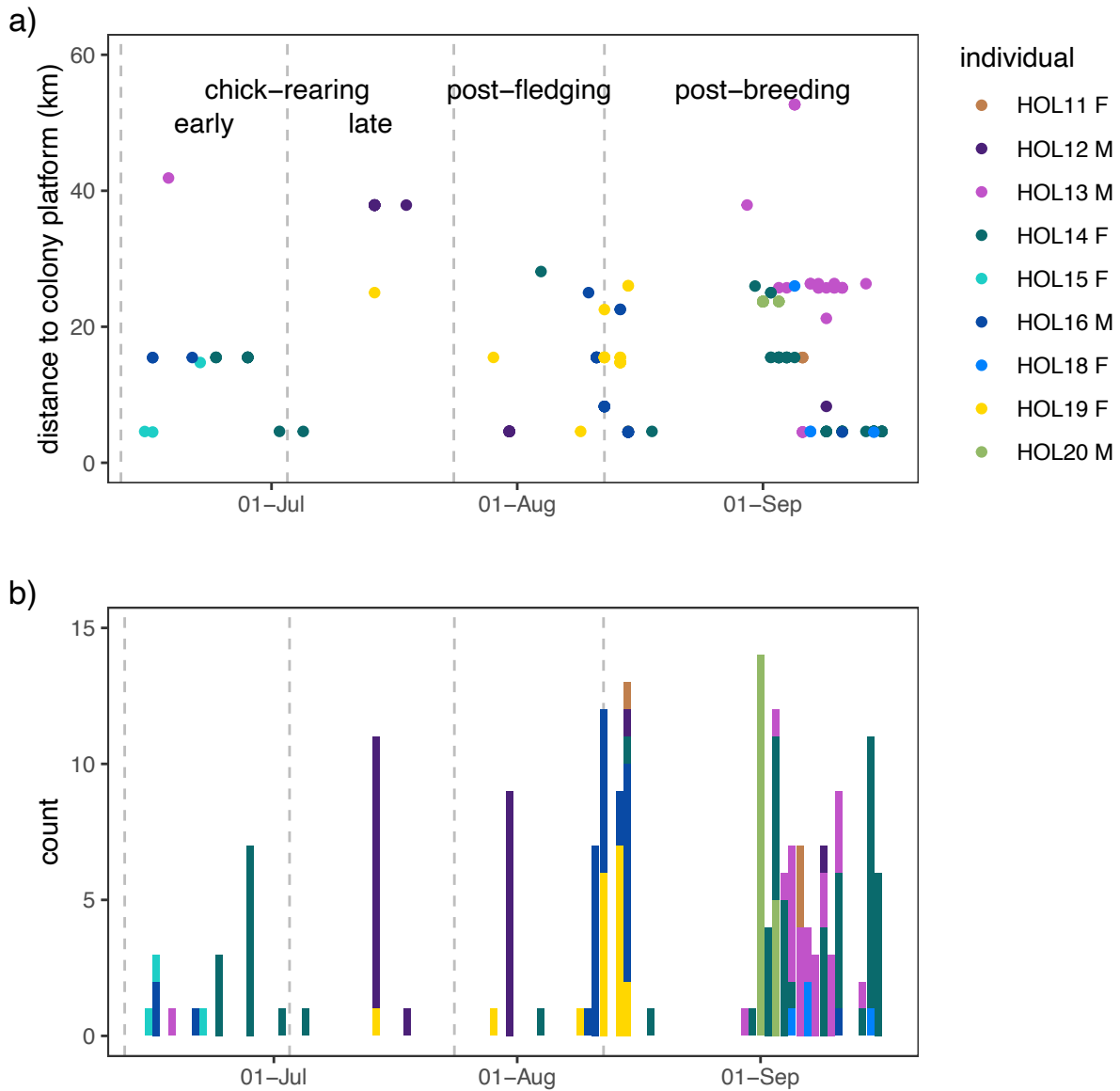


Figure 8. a) Distance to L7-B of platforms visited by the nine GPS-tracked Black-legged Kittiwake *Rissa tridactyla* in relation to date. b) Duration of stay (number of GPS-positions) per individual on platforms over time. Each GPS position should reflect a stay of ca. 15 minutes.

Discussion

We successfully GPS-tracked Kittiwakes breeding on an offshore platform in the Dutch sector of the southern North Sea, representing, to our best knowledge, the first published GPS-data from an offshore installation. Our main aims were to investigate the foraging range, foraging areas and connectivity with other offshore platforms.

Maximum trip distance

We found that foraging trips of Kittiwakes from the L7-B platform ventured in all directions and found evidence of shorter maximum trip distances during early chick-rearing than expected for a similarly-sized coastal colonies (Ainley *et al.* 2003; Hamer *et al.* 1993; Ostrand *et al.* 1998; Suryan *et al.* 2000; Humphreys *et al.* 2006; Kotzerka *et al.* 2010; Chivers *et al.* 2012; Paredes *et al.* 2014; Christensen-Dalsgaard *et al.* 2018; Osborne *et al.* 2020; Cleasby *et al.* 2023). The positive relationship between land cover and foraging ranges is in line with species-level studies on Northern Gannets *Morus bassanus* (Lewis *et al.* 2001) as well as across seabird species (Jovani *et al.* 2016). However, our result should be regarded with some caution. First of all, although the standard errors of the differences in ELPD are small and thus suggest ‘significant’ differences between the models, the absolute differences in ELPD are small (<4) and standard errors of the difference in ELPD can be over-optimistic when sample sizes are small (Sivula *et al.* 2020). In addition, our model does not consider individual-level variation, which can be substantial (Cleasby *et al.* 2023), or other sources of uncertainty in colony-level estimates. For example, foraging ranges can vary substantially between years as a result of food conditions (Hamer *et al.* 1993; Paredes *et al.* 2014; Osborne *et al.* 2020), but estimates of maximum trip distance from the same colony in multiple years were available for only part of the studies included here. Finally, the methods of obtaining colony-level mean maximum trip distances were not uniform across studies.

Evidence for density-dependent effects around a relatively small colony of only a few hundred breeding pairs, as in our study, seems surprising given that competition is expected to increase in intensity with colony size (Gaston *et al.* 2007; Coulson 2011). However, studies that link foraging range to colony size may be confounded by prey availability, i.e. larger colonies are likely found in areas with high prey availability (Gaston *et al.* 2007; Jovani *et al.* 2016). Conversely, small colonies are more likely in areas with relatively low prey availability (Ainley *et al.* 2003). This is where any density-dependent effect on foraging range is likely substantial and therefore likely to be detectable (Gaston *et al.* 2007). Whether prey availability could explain the relatively short foraging range of Kittiwakes during early-chick rearing at L7-B remains unclear, as we do not have the data to compare prey availability around L7-B to other similar-sized colonies. Limited nesting space at L7-B (but not necessarily at surrounding platforms) could also explain the relatively small size of the L7-B colony.

Alternatively, or in addition to decreased prey depletion, the relatively short foraging trips in all directions from the platform during early chick-rearing of the Kittiwakes breeding on L7-B compared to similar-sized colonies elsewhere could be explained by profitable foraging areas surrounding the platform. Within Kittiwake colonies, foraging ranges may expand in years with poor foraging conditions (Hamer *et al.* 1993; Paredes *et al.* 2014; Osborne *et al.* 2020), although Kittiwakes can also adjust foraging time in similar foraging ranges (Schlener *et al.* 2024). The L7-B platform, as well as other Dutch platforms known to support breeding Kittiwakes (Camphuysen & Leopold 2007), is positioned within the frontal zone between shallow, mixed water to the south and west and summer-stratified, deeper waters of the central North Sea (Baars *et al.* 1991) (Figure 1). This area, positioned roughly between depths of 30–40 m, is often referred to as the Frisian Front (but note that the same name is also used for the Natura2000 site just east of L7-B as well as the benthic ‘front’ within, supporting high zoobenthic diversity), and is known to support high primary productivity in summer, which propagates to higher trophic levels, including pelagic fish and seabirds (Baars *et al.* 1991). Here, Kittiwakes breeding at L7-B may profit from an abundance of pelagic prey, such as Sprat *Sprattus sprattus*, which can be abundant in summer in the area (Baptist *et al.* 2019). Outside the period of early chick-rearing, when longer trips occurred, the Kittiwakes’ trip bearings were distributed unevenly. Many trips ventured to the southwest (incubation) and north (late chick-rearing and post-fledging) of the platform, suggesting Kittiwakes targeted specific areas on these longer trips. The longer trips between 6 July and 14 August ventured

much further north than the Frisian Front frontal zone. In this area, the Oystergrounds, high densities of Kittiwakes are sometimes observed during aerial surveys (van Bemmelen *et al.* 2023). The northern part of the Oystergrounds, the Central Oystergrounds, is known to consistently hold substantial numbers of Common Guillemots *Uria aalge* in late summer and winter, and Razorbills *Alca torda* in winter. The area is also regularly occupied by thousands of Kittiwakes between August and February, but only hundreds during surveys in April and June (Fijn *et al.* 2021).

In addition to being close to an area of higher prey abundance at the Frisian Front, the offshore platforms themselves may create foraging opportunities by causing water turbulence in the wake of their jacket (Lieber *et al.* 2019; Schultze *et al.* 2020; Slingsby *et al.* 2022). In that case we might expect foraging positions to accumulate west and east of the platforms – the predominant direction of the tidal currents in the area around the L7-B platform. Although many positions between 100 and 500 m from the L7-B platform were indeed between east and southeast of the platform, there were also many positions between south and southwest of the platform, and low numbers from southwest, northwest to northeast. Positions around other platforms than L7-B also did not show a clear bimodal distribution, although a relatively large number of positions were to the east-southeast (Figure A5, see online Supplementary Materials).

In the absence of direct observations of the breeding stage of the tracked Kittiwakes in our study, our inference on maximum trip distances relative to other colonies partly relies on our estimation of the start of the chick-rearing period. We inferred this start from the steep drop in maximum trip distances, which has been described for Kittiwakes (Robertson *et al.* 2014; Cleasby *et al.* 2023), and later divisions of periods have been gleaned from Coulson (2011). Our estimates for maximum trip distances during chick-rearing may thus have been higher if hatching occurred earlier than 12 June, but maximum trip distances were also importantly smaller than those from Cleasby *et al.* (2023) when using all data up to 7 July or when using only the first part of what we assumed to be the early chick-rearing period.

More time in the colony during early chick-rearing

Overall, tracked Kittiwakes spent about half of their time in the colony, except for the early chick-rearing period when this increased to *c.* 62%. The time spent in the colony was estimated mainly from GPS-positions during the early chick-rearing period, but by the base station ‘in range’ in others. This is however unlikely to explain the higher percentage of time in the colony during early chick-rearing, considering that the base station likely registers the presence of GPS-loggers with higher accuracy than the GPS-loggers, which would lead to less rather than more records in the colony. That more than half of the time is spent in the colony during chick-rearing appears to contradict the findings by Coulson (2011), which state that during this period, parents are rarely more than a minute together at the nest. Possibly, birds were spending part of the time within 1 km from the platform, which were regarded in our analysis as ‘in colony’. Sex roles appear unable to explain the on average higher percentages of time in the colony during early chick-rearing, as our sample includes both males and females that spent similar and overlapping amounts of time in the colony. Instead, parents may spend more time at the nest to strengthen the bond with their chick or to defend the chick or nest site.

Longer trips during late chick-rearing and post-fledging periods

The use of long-lasting harnesses allowed for longer deployment periods than earlier tracking studies that covered the late incubation and early chick-rearing periods only (Christensen-Dalsgaard *et al.* 2018; Cleasby *et al.* 2023). Maximum trip distances increased during what we assumed were the late chick-rearing and post-fledging periods. The increase in the length of trips with progressing chick age likely

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reflects increasing chick food requirements. Such an increase has also been reported for other seabird species, such as Razorbill (Dall'Antonia *et al.* 2001) and Scopoli's Shearwater *Calonectris diomedea* (Cecere *et al.* 2013), but not for all species, as exemplified by Wandering Albatross *Diomedea exulans* (Weimerskirch & Lys 2000). The longer trips during the late chick-rearing and post-fledging periods of our tracked Kittiwakes led to a bimodal distribution of maximum trip distances during these periods. Such bimodal distributions are reported for many seabirds, including Kittiwakes (Christensen-Dalsgaard *et al.* 2018), where long trips allow parents to forage for self-maintenance and to replenish their body reserves (Chaurand & Weimerskirch 1994; Weimerskirch *et al.* 1994). However, in our study long trips were restricted to the late chick-rearing period and the post-fledging period. This suggests that in our study, parent Kittiwakes were not compromising their own condition during short trips in the early chick-rearing period, or that longer trips in the late chick-rearing and post-fledging periods reflect higher chick requirements. Future tracking studies with deployment periods covering the entire breeding season should reveal the generality and causes of these seasonal patterns in long foraging trips.

Return to the platform after the chick-rearing period

In our study, tracked Kittiwakes visited the nesting platform well into September. Adult Kittiwakes visit the colony daily after their chicks' final departure from the colony until the time the last chick of the colony fledges (Coulson 2011). In Britain, this usually occurs in the first week of August. In some years and colonies however, adults may visit the colony for much longer periods after the last chick has fledged - up to early November (Coulson 2011). Thus, visiting the L7-B colony until well into September is later than is usual for the species, but not extreme. Whether this timing is usual for this colony remains unclear, as our study spans only a single year.

Why would adults revisit their nesting platforms in September? As tracking data is largely lacking from this period, earlier inferences on behaviour of adults between fledging of their chick and final departure from the colony were based on observations in the colony (Coulson 2011). Our tracking data shows that during this time, adults made very short foraging trips – even shorter than during the early chick-rearing period. When relieved from the need to provision chicks at regular intervals, one might expect birds to make longer trips. However, the long period over which tracked adults visited the colony after the chick fledged, in combination with the very short foraging trips suggest that foraging opportunities in proximity to the platform may have been very good. Possibly, intra-specific competition close to the colony had decreased compared to early in the breeding season, if part of the colony had already been abandoned. However, only one of the tracked birds left well before early September, whereas the others left during the course of September. Another potential reason for the long period of colony visits is prospecting for the next breeding season and defending a nesting site (Ponchon *et al.* 2013). The increased frequency of visits to platforms other than L7-B in September could also represent prospective behaviour. Although the total time spent in the colony or in a stationary state elsewhere did indeed increase, these increases were relatively small. Finally, Kittiwakes may rest at platforms in September to save energy, considering they may face increased energy expenditure due to flight feather moult, that starts during breeding and continues into autumn and may be most intense in this period (Coulson 2011).

Visits to other platforms

GPS-tracked Kittiwakes breeding on platform L7-B regularly visited other platforms, with most visits lasting less than an hour. Visited platforms included two platforms where prospecting (L5-B) or breeding (L8-P) kittiwakes have been reported before (Camphuysen & Leopold 2007), but also many platforms for which we have no information on occupation by Kittiwakes. Breeding of Kittiwakes on platform L8-P has

been reported since 2000, with a maximum number of 32 pairs in 2006, but with no published counts since. In 2006, 11 prospecting adults were seen on platform L5-B, but no breeding birds. It is noteworthy that the platforms most visited by tracked Kittiwakes are abandoned and/or unmanned. It is tempting to speculate that these platforms also support Kittiwake colonies. In any case, the visits to other platforms by our tracked birds indicate that potential breeding sites are likely to be easily discovered by prospecting Kittiwakes.

Future directions

The 375 pairs of Kittiwakes breeding on platform L7-B and their at-sea distribution are not sufficient to explain the presence of tens of thousands of Kittiwakes in the Dutch sector of the North Sea in June and August 2018-2023, as estimated from aerial surveys (van Bemmelen *et al.* 2023). It thus remains unclear to what extent the Kittiwakes observed during these surveys are birds breeding on platforms, breeding outside the Dutch sector of the North Sea, and non-breeding immatures or floaters. Knowing the number of Kittiwakes breeding on platforms and their role in the dynamics of the North Sea meta-population is important, as platforms will eventually be decommissioned but are currently also considered for supporting breeding Kittiwakes to counteract the effect of mortality due to offshore wind farms. Future studies should therefore aim to estimate the number of Kittiwakes breeding on platforms, as well as their productivity and survival.

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