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Evidence of nocturnal migration over sea and sex-specific migration distance of Dutch Black-headed Gulls

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Avian migration is recorded over long distances, but some species winter much closer to their breeding sites or do not migrate at all. Specifically, the family of gulls *Laridae* shows great within and among species variation in migration. However, the migration ecology of many gull species is still unknown, even for abundant and widespread species such as the Black-headed Gull *Chroicocephalus ridibundus*. Here, we aimed to map the migration of Black-headed Gulls using GPS-tracking data from eight birds from a declining colony at Griend in the Dutch Wadden Sea to study migration routes and timing as well as wintering habitat of these birds. Furthermore, we used this GPS-data and 199 colour-ring resightings of adult birds from the same colony to study their wintering locations and habitat. The GPS-tagged birds migrated away from the Dutch Wadden Sea between mid-September and late November. All migrated in western to south-western directions to wintering areas at 130 to 560 km from the breeding colony. The GPS-tagged individuals wintered in The Netherlands, France and the United Kingdom and migrated towards these wintering sites both diurnally and nocturnally. The data indicate that most movements over the North Sea were nocturnal, whereas most migratory movements over land were during the day. Colour-ring data showed that females wintered significantly further away than males. We found no indications for differences in timing of migration between males and females and also no sex-specific preference for nocturnal or diurnal migration. We argue that the hitherto undocumented prevalence of nocturnal sea crossings calls for a better assessment of the potential risks of offshore wind energy developments in the North Sea. As such, this and new GPS-tracking data of Black-headed Gulls can aid in the conservation of this common and widespread species by providing novel insights in migration behaviour and the connectivity between breeding and wintering grounds.

Key words: wintering area, night, GPS-logger, colour-ring, habitat use, tracking, biologging, *Laridae*, *Chroicocephalus ridibundus*

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Avian migration, the seasonal movement of birds between breeding and non-breeding areas, has a long history in scientific research (Alerstam & Hedenström 1998, Berthold 2001, Newton 2008). Recent technological advances in tools to track avian migration have led to a remarkable increase in the number of studies to map the movement of birds in great detail (e.g. Kays *et al.* 2015). Despite the increase in the number of species for which tracking data is collected, fundamental baseline data on the migration ecology is lacking for many, including widespread and abundant species. Such baseline data includes the location of wintering grounds and migration routes as well as the seasonal and diurnal timing of migration, which forms crucial information for conservation efforts and impact assessment of anthropogenic developments such as offshore wind farms.

An example of a common species without high resolution tracking data of migration routes and wintering locations is the Black-headed Gull *Chroicocephalus ridibundus*. This is remarkable given its abundance in populated areas within its European range. Black-headed Gulls breed colonially and have a widespread breeding range which stretches from Eastern Canada, Greenland and Iceland, across most of Europe (with a southern limit in the Mediterranean), into far eastern breeding grounds in Kamchatka, Russia (del Hoyo *et al.* 1996, Keller *et al.* 2020). About 100,000 pairs of Black-headed Gulls breed in The Netherlands, but numbers have recently been decreasing significantly with up to 5% per year (Sovon Vogelonderzoek Nederland 2021). The main reason for this decline is thought to be unsustainably low reproduction rates due to predation and food shortage (Majoer *et al.* 2018). Specifically, in the Wadden Sea, predation of clutches and hatchlings by European Herring Gull *Larus argentatus argenteus* seems to be a major contributing factor. Whether Black-headed Gulls also face threats during migration and on their wintering grounds is difficult to assess since accurate information on flight routes and migratory behaviour is lacking.

The migratory behaviour (distance and timing) of Black-headed Gulls has long been subject of interest and study, but substantial parts of their migration behaviour were unknown for a long time. Tollenaar (1917) already wondered about the migration patterns of this species, but it was only until the studies of Taapken (1960), Platteeuw *et al.* (1985) and Platteeuw (1987) that the first hypotheses on the migration of these gulls were more explicitly postulated. Taapken (1960) suggested that the majority of Black-headed Gulls that breed in The Netherlands migrate to the United Kingdom (UK hereafter), France, Spain, Portugal and Northern Africa, whilst birds from Fennoscandia and Eastern Europe winter in The Netherlands. He specifically referred to juveniles from the Czech Republic that

follow rivers to get to The Netherlands. Platteeuw (1987) based his findings on Black-headed Gull migration mainly on data collected at coastal migration observation sites ('seawatches') and observations from gas platforms in the North Sea. He suggested the existence of two migration peaks in spring (February/March, April) and two in autumn (July, October), where each peak consisted of groups of birds with a common origin, breeding status or age to migrate during those peaks. He also suggested that the occurrence of migration peaks in The Netherlands might be food driven, such as attraction of gulls to spawning Smelt *Osmerus eperlanus* or deteriorating food conditions in inland pastures.

Platteeuw *et al.* (1985) were among the first to flag the occurrence of North Sea crossings of Black-headed Gulls based on observations from platforms in the southern North Sea. Although substantial numbers of Black-headed Gulls must migrate over the North Sea towards wintering areas in the UK (Wernham *et al.* 2002), offshore migratory movements across the (Dutch) North Sea have been recorded only very sparsely. Based on ship-based seabird surveys, Camphuysen & Leopold (1994) reported scattered offshore records in July (Oestergronden) and October (Doggersbank, Nord-schillgrund and Terschellingerbank regions). Moreover, small numbers of birds were recorded offshore in April, probably reflecting late migrants heading for more easterly or northerly breeding areas than The Netherlands. Further north in the North Sea, incidental observations from oil and gas platforms of migrating Black-headed Gulls were recorded in October (Tasker *et al.* 1986), probably concerning gulls migrating from Norway to the northern UK.

Since these early observational studies, multiple (colour-)ring studies of Black-headed Gulls in Europe have led to a better understanding of the movements and wintering areas (Horton *et al.* 1984, Christmas *et al.* 1986, MacKinnon & Coulson 1987, Ivanauskas *et al.* 1997, Majoor *et al.* 2005, Jurinović & Kralj 2013). These studies showed that Black-headed Gulls are partial migrants, with part of the individuals traveling over short to long distances, whereas others only perform dispersive (<100 km) movements near their breeding sites. Which part of the population migrates, and why, is unknown. What we do know is that Black-headed Gulls breeding in The Netherlands winter mainly in the UK, Belgium, France and Spain (VogeltrekAtlas 2021), yet high-resolution data of their wintering sites and migratory routes has not been published.

For long, tracking devices were too heavy to be deployed year-round on Black-headed Gulls. With the increasing miniaturization of tracking technology, a few studies of local habitat use have now shown the feasibility of tracking Black-headed Gulls (Gorke & Brandl 1986, using VHF-tags, Jakubas *et al.* 2020, using GPS-loggers). This opened the possibility to reveal the migration behaviour of this declining species in greater detail. One of the urgent knowledge gaps that high-resolution tracking data could fill is, for example, the potential interaction of migrating Black-headed Gulls with offshore wind farm developments. Currently, Environmental Impact Assessments for offshore wind farms in the North Sea are based on day-time seabird surveys only (Leopold *et al.* 2014). And although many Black-headed Gulls from Europe winter in the UK and must therefore migrate over the North Sea, the numbers observed during these surveys are very low. Nocturnal migration, which is

known from other gulls, terns and waders (e.g. Lack 1959, 1963, Camphuysen 1992), could explain this discrepancy, yet the importance of nocturnal migration for Black-headed Gulls is unknown.

The occurrence of nocturnal migration in Black-headed Gulls has been postulated, for example based on observations of migration late in the evening during dedicated migration counts (Lensink *et al.* 2002), but movements in the evening may also refer to movements towards nocturnal roosting sites instead of migration flights. True nocturnal movements of Black-headed Gulls have been established using continuous sound recording of birds passing overhead by night ('nocmigging'), an activity only recently picking up popularity among birders. 'Nocmigging' at Dutch inland sites shows three peaks, corresponding to diurnal migration counts: late February – early April, mid-June – mid-July and from mid-October to early November (www.trektellen.nl; accessed 27/1/2021). In contrast, during nocturnal 'observations' at Offshore Wind farm Egmond aan Zee (OWEZ), calls from Black-headed Gulls were only heard in autumn, generally between 0:00 and 3:00, but not in spring (Krijgsveld *et al.* 2011), suggesting a difference in call prevalence between the two seasons and between habitats (coastal vs. inland).

The first aim of our study was to document when Black-headed Gulls migrate during the year and whether migratory flights took place during the day or night. Based on sightings of migrating gulls in the evening in The Netherlands, we expected that at least part of our birds would migrate at night to their wintering locations. The second aim of this study was to map wintering grounds and test for differences between sexes, as suggested by previous ring recoveries. To answer these two questions, we tracked 11 Black-headed Gulls of known sex from the largest breeding colony in The Netherlands (Griend, Wadden Sea) with GPS-loggers between two breeding seasons and combined this data with winter-resightings of 199 colour-ringed and sexed adults from Griend.

METHODS

Study site

The island of Griend (53°14'N, 5°14'E; 70 ha) is an important breeding area for various coastal bird species within the Natura2000 Special Protection Area 'Wadden Sea'. The island was home to 14,607 breeding pair of Black-headed Gull in 2019.

GPS-tracking

A total of 11 adult Black-headed Gulls were captured on the nest using a bird-triggered clap-net or walk-in trap on 19 May 2019. At this date, all birds except one were incubating three eggs; the one individual had two eggs. Based on observations by the local wardens of settling birds, all captures were done on nests where the eggs were approximately 10 days before hatching. All birds were fitted with a white coded colour-ring with four digits. Sex of these birds was determined based on head length and bill depth measurements during ringing following the equation of Palomares *et al.* (1997). All were also fitted with a GPS logger (Ecotone, model PICA, c. 4.5 g, solar-powered, L×W×H: 50×5×10 mm) attached to a harness made of Teflon. GPS loggers, along with harness and rings (6.3

g), weighed less than 3% of the total weights of all birds (average body mass: 242 ± 16.4 g (\pm SD; range: 220–270)), to a maximum of 2.9% in the lightest bird (body mass: 220 g). Total handling time between capture and release was between 10 and 20 min per bird.

GPS loggers were programmed to collect the latitudinal and longitudinal position based on the information from GPS satellites whenever outside the range of the base station. The base station was located close to the colony and stored data downloaded automatically from the GPS loggers via UHF when they were within range (c. 200–500 m). The loggers were equipped with a build-in solar panel for charging the internal battery. The initial scope of this work was to study foraging movements of Black-headed Gulls to infer habitat use during the breeding season. In 2020, nine gulls of our original sample returned to breed close to the base station and eight uploaded data of the non-breeding season.

To balance the advantage of more data and the risk of battery drainage considering the sun condition during the light conditions in summer at 53°N, three loggers were programmed to collect GPS-fixes throughout the day (24 h), whereas the remaining loggers collected GPS-fixes during 12 h each day (between 6:00 and 18:00 local time). GPS-loggers recorded positions at 60-min intervals.

Tag performance and return rate

In total, 9 out of 11 individuals returned to the colony and 8 loggers uploaded data remotely to the base station. A low battery voltage is the most likely cause of the upload failure of the ninth logger, the logger made contact initially, but no power was left to upload data. Some of the loggers had long periods with no or very few positions logged due to insufficient battery voltage. However, the positions that were recorded did yield information on wintering locations, and partially on autumn- and spring migrations.

With only 2 out of 11 loggers not recorded back in the colony in 2020, the return rate (0.82) was within the range of average annual apparent survival rates of 0.8–0.9 reported for adult Black-headed Gulls (Prévot-Julliard *et al.* 1998, Majoor *et al.* 2005). Disappearance of these two missing individuals can have several causes. They may have died, but we cannot exclude the possibility that these birds did not choose Griend as a breeding site. They could also have bred on Griend, but not within c. 500 m of the base station and thus be out of reach of downloading data. Another option could be that the birds lost their loggers somehow. A further option could be that the loggers were not working anymore in the following season. Due to very limited hours of sunlight during winter, the batteries easily go below a critical voltage for maintaining active, causing damage to the battery. To illustrate this, we noted the retrieval of one of our loggers from a fresh dead Black-headed Gull in summer 2021. This logger was not recorded by the base station in 2020 and 2021. Connecting the logger from the base station revealed that the logger had died in the winter of 2019/2020. So, either this bird did not breed in the vicinity of the base station in 2020 and 2021, or did so but with a defective logger on its back.

Colour-ringing

In the past 10 years, 491 adult (242 male, 249 female) Black-headed Gulls were colour-ringed at Griend with field-readable inscribed Darvic colour rings. To calculate migration distances and directions of colour-ringed birds, all recoveries and resightings during November–February from the years between 2013 and 2020 were selected.

Statistical analyses

After the breeding season, the base station was retrieved from the island and the data were downloaded. All data were analysed in R v. 4.0.2 (R Core Team 2020). Habitat characteristics of GPS-fixes to study species were determined using data from the Corine Land Cover 2018, v. 2018_20 (<https://land.copernicus.eu/pan-european/corine-land-cover/clc2018?tab=mapview>). This layer was combined with satellite imagery available at Google Maps to study habitat features of GPS locations of tagged Black-headed Gulls.

Migration events were defined as a flight of more than 100 km in autumn or spring from and towards the Dutch Wadden Sea. Start of autumn migration was defined as the time when individuals departed the Wadden Sea area permanently (Figure 1), as this excluded all post-breeding movements within or close to the Wadden Sea. The end of spring migration is defined as the time of the last movement before entering the Wadden Sea for the first time, as this excluded pre-breeding movements close to the Wadden Sea (Figure 1). In six of sixteen cases, no details of the timing and speed of a migration bout could be determined because no positions were taken in the two days before or after the actual migratory flight.

To compare prevailing wintering areas between sexes and between colour-ringed and GPS-tagged birds ('mark type'), migration distance and migration direction were compared. Uniformity of migration directions was assessed using Rayleigh tests. Differences in the response variable 'migration direction' were compared between sexes and mark type as explanatory variables using the non-parametric Watson U^2 test, since this test gives robust results even with dissimilarity in the concentration parameter, as was the case in our data based on a Watson-William test. To compare migration distances between sexes, Generalized Linear Models with a gamma distribution for the response variable were used as migration distances were strongly left skewed.

RESULTS

Tracking data

From the 11 Black-headed Gulls in 2019, GPS data from eight loggers were successfully uploaded to the base station in spring 2020. In total, 4812 GPS-positions were recorded between 15 September 2019 and 10 April 2020 (Table 1).

Migration

After spending the post-breeding period in and around the Wadden Sea, autumn migration of GPS-tagged Black-headed Gulls was initiated around mid-September (one female), early October (two

males, two females) and late November (one male, one female; Figure 1). Unfortunately, some of the migrations were not completely recorded due to low battery voltage. Spring migration was more synchronized between the GPS-tagged gulls, with all birds flying back from the wintering grounds to the Wadden Sea in the course of March (Figure 1).

Out of 16 migratory movements (eight birds, autumn and spring migration) positions during migration were recorded for 10 flights. Based on the migrations for which detailed data was recorded, migration was relatively fast and direct, with most migrations taking only a single night or day (Figure 1, 2, Table 2). Six of the 10 flights were during the night, and four during the day (Table 2). In two gulls, both autumn and spring migrations were diurnal and in one gull both movements were nocturnal. Mixed migration strategies (diurnal in one season, nocturnal in the other and *vice versa*) were not recorded. Five of the tracked birds crossed the North Sea when migrating to their wintering grounds and/or back. For six out of the ten sea crossings we could determine whether they were performed during the day or night. Five crossings were during the night and only one crossing was during daytime. Among terrestrial migrations, three were performed during the day, none during the night, and three could not be assessed. Both sexes migrated during night and day. Females were more often recorded to travel at night (four out of six migrations) whereas males were more often recorded to travel during the day (three out of four migrations; Table 2).

Wintering areas

In total, 199 resightings were obtained during the winter from 199 individual Black-headed Gulls that were colour-ringed at Griend, with a sex ratio of 41% females to 59% males. The direction from the ringing location to the recovery position of the colour-ringed birds was -135° (Figure 3) and differed in distribution between sexes (Watson $U^2 = 1.3383$, $P < 0.001$). Females were resighted significantly further away than males (median: 844 km vs. 444 km, $\beta_{\text{male}} = -0.4$, $df = 197$, $P < 0.001$; Figure 3).

Black-headed Gulls with GPS-loggers were recorded at a maximum distance of 560 km from the breeding colony (Table 1, Figure 1). Maximum distance of the wintering site to the colony remained stable in most birds indicating no major movements during the wintering period. Only one bird moved around during winter (Figure 1).

Five of the GPS-tagged gulls wintered in the UK in generally three different regions. Three females spend most of the winter in Essex, Suffolk and Norfolk, one male resided north of Leeds and another male in Greater Liverpool, although the logger of this latter bird only started working again in February. Two male Black-headed Gulls wintered in The Netherlands. The last female wintered in northern France where she was found in the Baie de la Somme until mid-December before moving to an area south and east of Paris.

Black-headed Gulls used a wide variety of habitat types with some individuals recording almost 70% of their GPS-fixes on the wintering grounds in one habitat type (Figure 4). Overall, more than 55% of GPS-fixes were recorded in agricultural habitat. Over 20% were recorded in inland waters (Figure 4) where birds spend the night on lakes and ponds. Urban habitat made up for 12% of all GPS-fixes and some gulls were recorded spending the night on roofs of large buildings, such as

industrial buildings and airports. A total of 8% of fixes was found in maritime wetlands, such as estuaries and intertidal flats. The remaining 4% of fixes were recorded at sea and in vegetated natural habitat. Females were proportionally more found in agricultural fields and grasslands (59% of fixes from females vs. 41% from males) whereas males used similar habitats but spent much more time in urban habitat (38% in males vs. 5% in females). The bird that wintered in France used agricultural areas during the day, but also visited three different refuse dumps and a water treatment plant multiple times during the winter. See Supplementary Material for some examples of these different habitats.

The distribution of migration directions differed significantly from uniformity ($\bar{R} = 0.8192$, $P < 0.001$), also within sexes (males: $\bar{R} = 0.8463$, $P < 0.001$, females: $\bar{R} = 0.9405$, $P < 0.001$). The distribution of directions from Griend to the wintering location differed between resightings of colour-ringed birds and winter-centroids of GPS-tracked individuals (Watson $U^2 = 0.2284$, $P < 0.05$).

DISCUSSION

This study is the first to successfully track the migration of individual Black-headed Gulls using GPS-loggers and yields novel insights in their migration and wintering behaviour. We found that after spending the post-breeding period within the Wadden Sea, birds with GPS-loggers migrated to their wintering areas between late September and mid-November. Black-headed Gulls migrated in a south-western direction to wintering grounds up to 2500 km away; individuals with GPS-loggers wintered much closer in the UK ($n = 5$), France ($n = 1$) and The Netherlands ($n = 1$). Based on the colour-ringed birds, females migrate further (median: 844 km) than males (median: 444 km), but our sample size of GPS-tagged birds is too small to statistically compare these results. Migration of birds with GPS-loggers usually took one or two days, with most migration bouts taking only a single day or night. Interestingly, most North Sea crossings took place at night. Our findings provide novel insights in the connectivity between breeding and wintering grounds and nocturnal migration behaviour of Black-headed Gulls, and offer leads for further studies on life-cycle dependent population bottlenecks, which is important considering the species' current decline in The Netherlands.

Migration

Our tracking data confirms earlier suggestions that Black-headed Gulls wintering in the UK do not cross at the shortest oversea route (which would be in the Channel) but migrate straight from The Netherlands to the UK (Platteeuw 1987). Offshore migratory movements across the (Dutch) North Sea have been recorded only very sparsely. The paucity in records of migrating Black-headed Gulls across the North Sea is remarkable given the large numbers of individuals wintering in the UK (c. 2.2 million; Banks *et al.* 2007), that originate largely from more easterly breeding areas, including The Netherlands (Wernham *et al.* 2002). Potential explanations for this apparent discrepancy are that migrants spread over a broad migration front, resulting in overall low densities, migrate at great altitudes, and/or perform these sea-crossing primarily during the night.

Our results indicate that most North Sea crossings by Black-headed Gulls are nocturnal. Black-headed Gull migration behaviour has been mainly studied by diurnal migration counts (Platteeuw *et al.* 1994, Lensink *et al.* 2002) and continuous sound recording or ‘nocmigging’ (www.trektellen.nl; accessed 27/1/2021). Despite showing the occurrence of nocturnal movements in Black-headed Gulls, none of the aforementioned data sources can quantify the relative occurrence of diurnal and nocturnal migration, as migration counts record only diurnal migration and ‘nocmigging’ only nocturnal migration. Therefore, our assessment of the ratio between diurnal and nocturnal migration in Black-headed Gulls is the first of its kind. Considering our small sample size, further GPS-tracking of Black-headed Gulls is required to provide a more robust estimate of the ratio between nocturnal and diurnal migration.

If indeed the migration of Black-headed Gulls occurs predominantly at night, this has important consequences for assessments of the effects of human activities offshore, such as the construction of wind farms. Due to the absence or low prevalence of the species in survey data, Black-headed Gulls are currently not accounted for in Environmental Impact Assessments in The Netherlands (Gyimesi *et al.* 2018). However, considering Black-headed Gulls regularly fly at rotor height (Krijgsveld *et al.* 2011), they will risk collision with turbines when navigating through offshore wind farms – especially at night. Considering the planned expansion of offshore wind farms in the (southern) North Sea (Gyimesi *et al.* 2018), the substantial numbers of Black-headed Gulls crossing the North Sea to winter in the UK (Wernham *et al.* 2002) and that most of these crossings appear to be performed at night, we propose that the potential cumulative effects of offshore wind farm developments on Black-headed Gull populations should be carefully re-assessed.

Timing of the autumn migration of Black-headed Gulls with GPS-loggers was spread over several months whereas spring migration took place within one month. The more synchronized arrival at the breeding areas suggests stronger selection on timing of migration in spring than in autumn, which is conform the general pattern among species (Newton 2008). The seasonal timing of migration of our GPS-tagged Black-headed Gulls, with spring migration in March–early April and autumn migration in October–November, corresponds with results from coastal migration counts (Platteeuw *et al.* 1994). The coastal migration peak in October concerns mainly adult birds, is generally only visible along the coast and often coincides with colder periods (Platteeuw 1987). An earlier migration peak, in the 2nd half of July, mainly concerns 1st cy birds, 2nd cy birds that recently finished moult and presumably also adults that failed breeding (Platteeuw *et al.* 1994). However, while all our GPS-tagged birds probably failed breeding in 2019 due to predation of eggs and hatchlings by Herring Gulls, most individuals migrated in October and November. Our data thus shows that failed breeders not necessarily start migration early but might stay for similar lengths of time as successful breeders. This might be the consequence of local weather regimes regulating the onset of migration (e.g. Shamoun-Baranes *et al.* 2006, Jurinović & Kralj 2013) or may allow them to complete their post-natal moult, which takes about three months (Olsen & Larsson 2003), before migration.

Wintering areas

The main wintering areas of our colour-ringed and GPS-tagged Black-headed Gulls were in the UK, The Netherlands and in France, thus in a western and south-western migration direction. This direction is in line with the ring recoveries of breeding adult Black-headed Gulls ringed elsewhere in The Netherlands and retrieved during the winter months (Vogeltrekatlas 2021). That more than half of our GPS-tagged individuals and about one-third of the colour-ringed individuals wintered in the UK reaffirms the importance of the UK for Dutch Black-headed Gulls (Horton *et al.* 1984, synthesis by Wernham *et al.* 2002).

Despite the similarity in migration direction between colour-ringed and GPS-tagged Black-headed Gulls in this study, we also found indications for differences between the two samples in migration distance. The GPS-tagged birds stayed relatively close to the breeding area. Sample sizes of GPS-tagged birds are too small to give definite answers, but a potential explanation could be a shorter migration distances due to a negative tag effect. These effects are, however, generally more pronounced in smaller bird species and with higher relative tag-loads (Barron *et al.* 2010). Another explanation could be a confounding effect of the prevalence of different weather conditions and consequently further wintering locations between the study period of colour-ringing (2013–2020) and GPS-tracking (2019/20 only; e.g. Visser *et al.* 2009, Machín *et al.* 2015).

The majority of the GPS-tagged birds mostly visited agricultural areas and coastal estuaries, where they are less likely to be seen by bird watchers than in urban areas. However, several Black-headed Gulls with GPS-loggers regularly visited densely populated areas (Rotterdam, Amsterdam, Paris, Liverpool, Great Yarmouth, Norwich) where many birders and ring readers reside. That none of these birds have been reported during the 2019–2020 non-breeding period is therefore remarkable. Considering the high fidelity to wintering sites from year to year (Wernham *et al.* 2002), the lack of resightings probably highlights the bias in encounter probabilities towards individuals using specific sites where colour-rings can easily be read.

Our Black-headed Gulls used a wide variety of habitat types, with females found predominantly in agricultural fields and grasslands and males more in urban habitat. Sex-specific differences in habitat use during migration has been found in gulls before (e.g. Baert *et al.* 2018). Our limited sample sizes and field data cannot shed light on potential drivers of the observed patterns but niche specialization and competition, as suggested for breeding Black-headed Gulls by Jakubas *et al.* (2020), is a likely explanation. Urban environments might benefit the larger males over the smaller females, but future tracking data, aimed at collecting detailed movement data at wintering sites, might shed more light on sexual differences in habitat selection and its potential drivers.

Conclusion

Our study shows that Black-headed Gulls tagged with GPS-loggers in the largest colony in The Netherlands migrated in western and south-western directions to wintering sites at 130 to 560 km from the breeding colony. Colour-ringed birds from the same colony migrated in similar directions and were recorded up to 2500 km away from the colony. Females wintered further away than males. We also revealed that, although migratory movements took place both during the day and at night,

most North Sea crossings took place at night, which can have important ramifications for assessment of the potential impact of offshore human developments.

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SAMENVATTING

Vogeltrek vindt vaak over grote afstanden plaats, maar sommige soorten overwinteren dichtbij hun broedplaatsen of trekken helemaal niet weg. Ondanks de enorme toename van het aantal soorten waarvan individuen zijn gevolgd met steeds kleinere en meer geavanceerde methoden, zijn er nog altijd heel algemene soorten waarbij basiskennis over het trekgedrag ontbreekt. Een voorbeeld daarvan is de Kokmeeuw *Chroicocephalus ridibundus*, een wijdverspreide en veel voorkomende broedvogel in Nederland. In dit artikel beschrijven we het trekgedrag en de overwinteringslocaties van acht volwassen Kokmeeuwen die met GPS-loggers waren uitgerust. Alle meeuwen waren gemerkt in de kolonie op Griend in de Waddenzee, de grootste kolonie van Nederland. Daarnaast hebben we in dezelfde kolonie 199 meeuwen van kleurringen voorzien. De vogels met GPS-loggers bleven tot oktober in de Nederlandse Waddenzee, sommige zelfs tot eind november, alvorens ze in westelijke en zuidwestelijke richtingen vertrokken naar overwinteringsgebieden die tussen de 100 en 500 km van de broedkolonie lagen. Deze vogels overwinterden in Nederland ($n = 2$), Frankrijk ($n = 1$) en het Verenigd Koninkrijk ($n = 5$) en migreerden zowel overdag als 's nachts naar deze overwinteringsgebieden. Interessant is dat de meeste bewegingen boven de Noordzee in de nacht plaatsvonden, terwijl de meeste trekbewegingen over land overdag waren. De kleurringgegevens lieten zien dat vrouwtjes verder weg overwinterden dan mannetjes. Er was geen verschil in het tijdstip van migratie tussen mannetjes en vrouwtjes, ook werd geen seksuele voorkeur voor nacht- of dagtrek gevonden. We stellen dat het tot dusver niet gedocumenteerde voorkomen van nachtelijke trekbewegingen over zee vraagt om een nadere inschatting van de potentiële risico's van bijvoorbeeld offshore windenergieontwikkelingen in de Noordzee. Zo kunnen deze en nieuwe GPS-trackinggegevens van Kokmeeuwen helpen bij het behoud van deze algemene maar afnemende soort.

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PHOTOS



Part of the colony of Black-headed Gulls on the island of Griend in the Dutch Wadden Sea, surrounding the wardens' cabin (photo Thea Smit, 20 May 2020).

TABLES

Table 1. Summary of tracking data per individual between 15 September 2019 and 10 April 2020 (208 days). Arrival and departure dates refer to the last and first position inside the Wadden Sea area (Figure 1). The departure date of logger E could not be assessed due to logger failure in autumn and early winter.

Individual	Duty cycle	N days with data	N positions	Departure	Arrival	Maximum distance from colony (km)
A (female)	24 h	135	782	20/9/2019	18/3/2020	561
B (female)	24 h	65	570	3/10/2019	24/2/2020	368
C (female)	6:00–18:00	155	1039	20/9/2019	1/4/2020	271
D (female)	6:00–18:00	123	829	20/11/2019	18/3/2020	270
E (male)	6:00–18:00	65	490	4/10/2019	7/3/2020	462
F (male)	24 h	49	357	–	16/3/2020	553
G (male)	6:00–18:00	97	483	13/11/2019	14/3/2020	162
H (male)	6:00–18:00	79	262	2/10/2019	12/3/2020	126

Table 2. Summary of migration periods in autumn 2019 and spring 2020 of GPS-tagged Black-headed Gulls from Griend and whether migration took place across the North Sea and (mainly) nocturnally or diurnally.

Individual	Sea crossing	Autumn (nocturnal/diurnal)	Spring (nocturnal/diurnal)
A (female)	no	20/09 – 7/10 (diurnal)	11/03 – 18/03 (diurnal)
B (female)	yes	3/10 – 5/10 (nocturnal)	22/02 – 24/03 (unknown)
C (female)	yes	20/9 – 21/9 (nocturnal)	31/03 – 01/04 (nocturnal)
D (female)	yes	20/11 – 29/11 (unknown)	17/03 – 18/03 (nocturnal)
E (male)	yes	04/10 – 06/10 (unknown)	05/03 – 07/03 (diurnal)
F (male)	yes	not recorded	15/03 – 16/03 (nocturnal)
G (male)	no	13/11 – 20/12 (unknown)	13/03 – 14/03 (unknown)
H (male)	no	02/10 – 02/10 (diurnal)	08/03 – 12/03 (unknown)

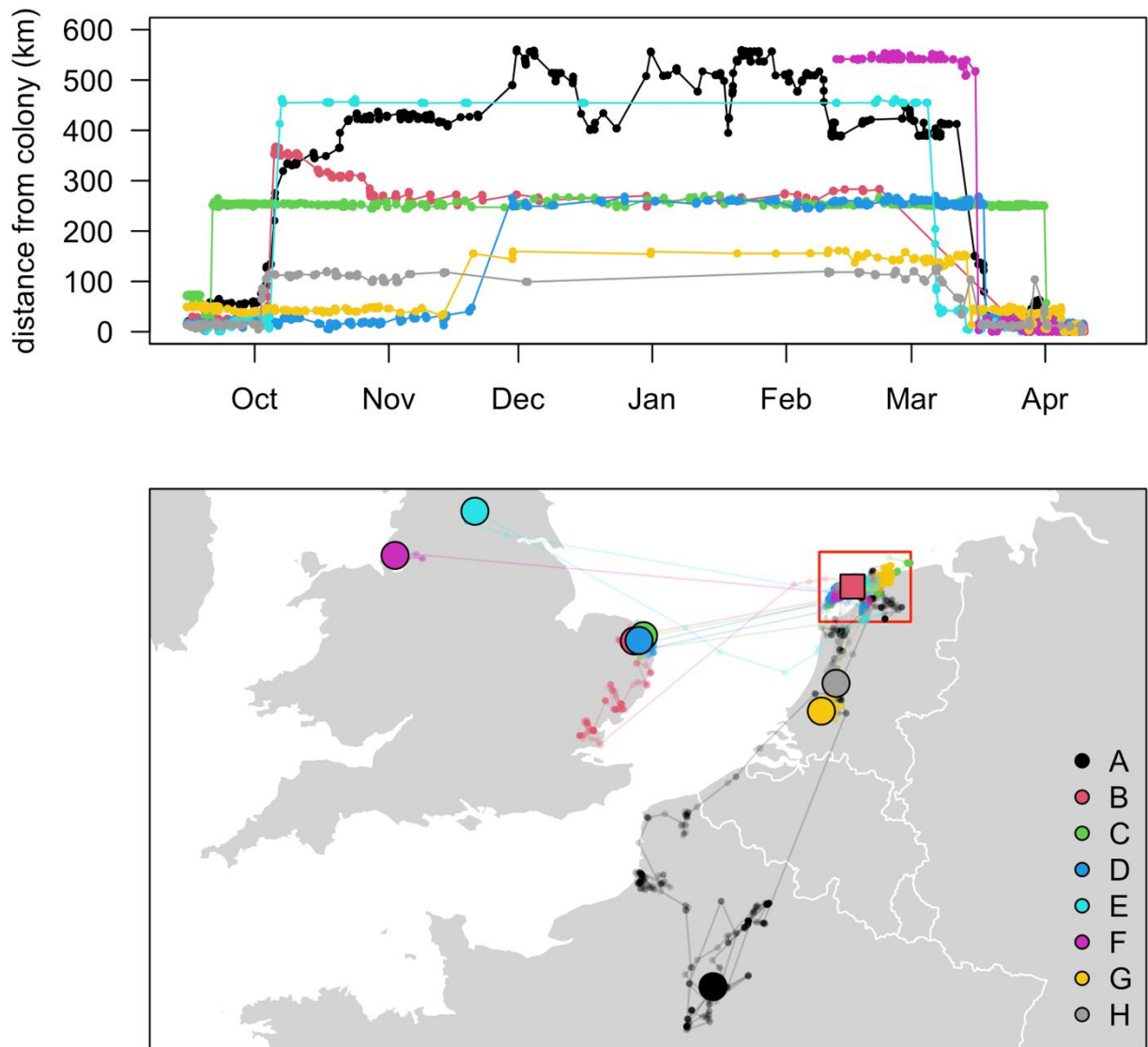


Figure 1. Distance of eight Black-headed Gulls with GPS-loggers from the colony at Griend (red square in lower graph) in relation to date (upper graph). Ticks on the x-axis are on the 1st day of each month. Dots represent GPS-fixes, which are connected by straight lines. Note that some loggers took fewer points in winter, when short daylight periods caused low battery voltage. Crossing the red outline of the Wadden Sea area was used to identify migration events. Lower graph shows a map with the distribution of logged positions (small dots) in the same time frame, and the median positions in December–February (large dots) of the same birds. Data from each individual is indicated by a different colour.

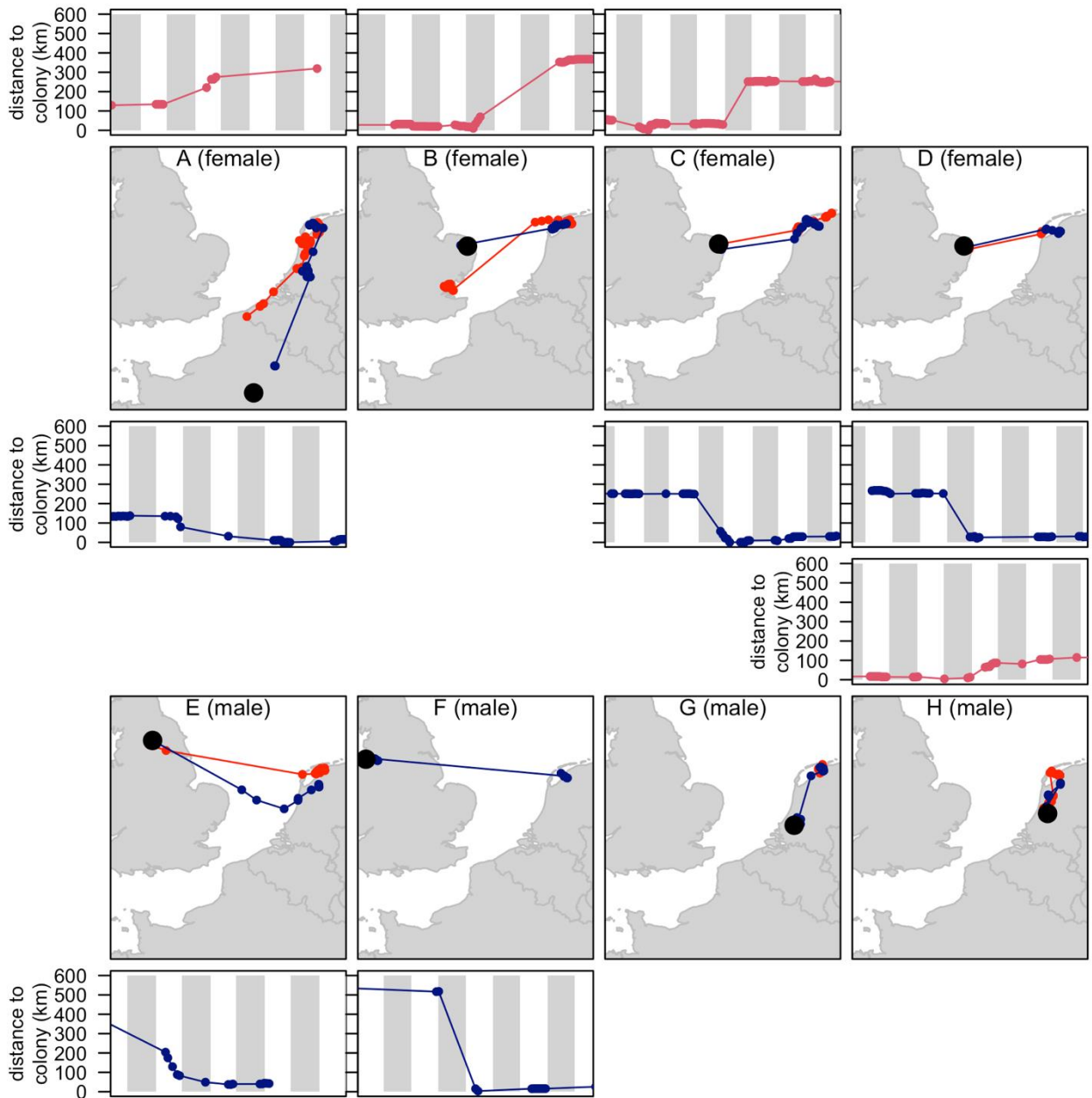


Figure 2. Migration routes (middle) in autumn (red) and spring (blue) of GPS-tagged Black-headed Gulls from The Netherlands, with wintering location (from Figure 3) shown as a black dot. Migration progress is shown as distance to the colony plotted against time for the autumn of 2019 (upper panels, red) and the spring of 2020 (lower panels, blue) for all loggers in which the migration trajectory was recorded in sufficient detail to reveal whether movements were predominantly during the night (grey background in graphs) or day (white background).

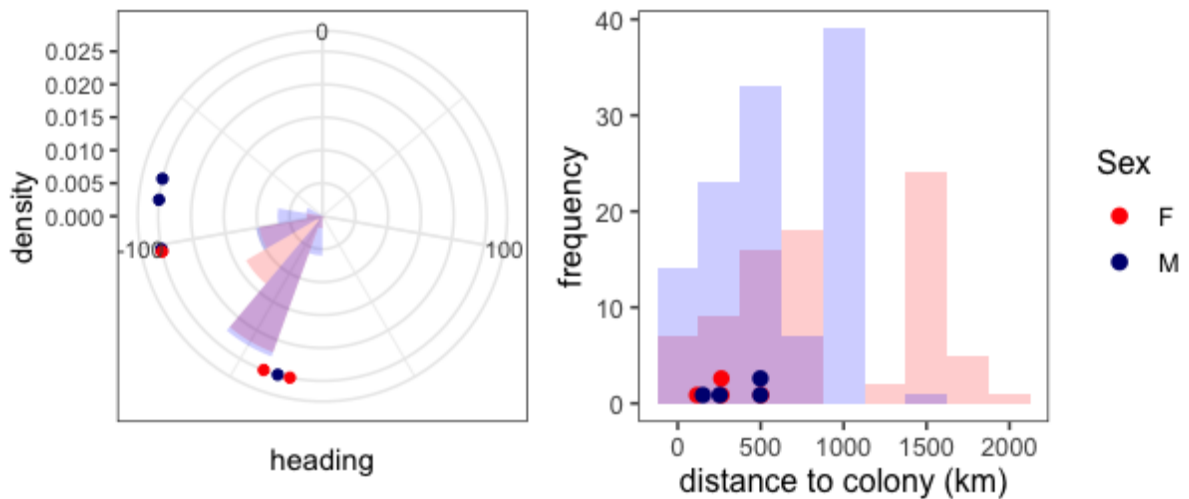
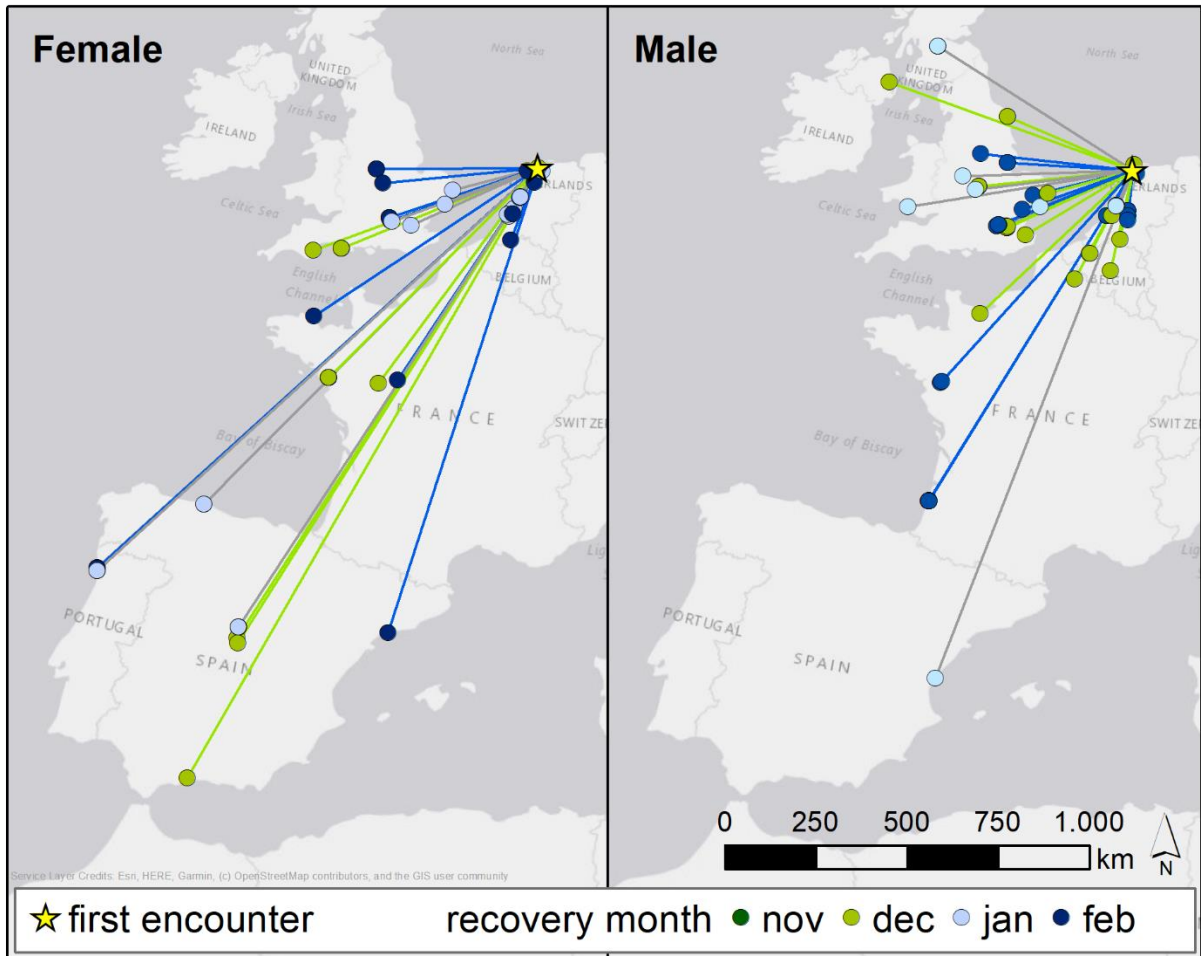


Figure 3. Recovery/resighting locations per month (dots, upper panel), direction (left lower panel) and distance (right lower panel) in November–January of Black-headed Gulls that were colour-ringed as adults at Griend (yellow star) split for females and males. Dots in the lower panel show the direction (left) and distance (right) of winter centroids of the eight GPS-tagged Black-headed Gulls within the same bins as used for the colour-ringed birds.

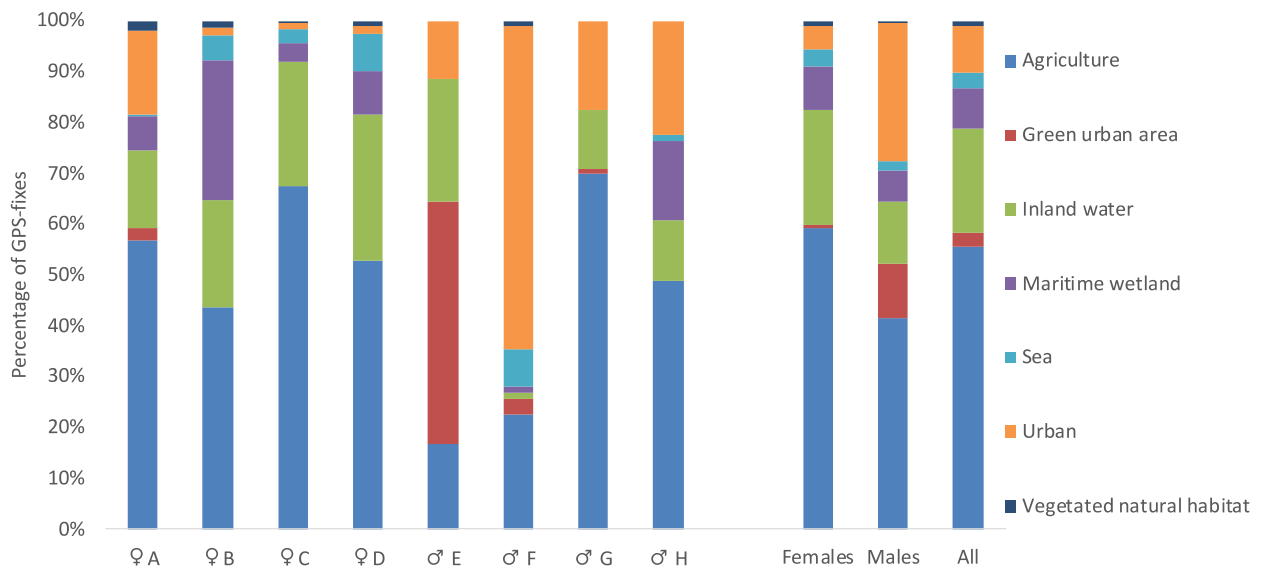
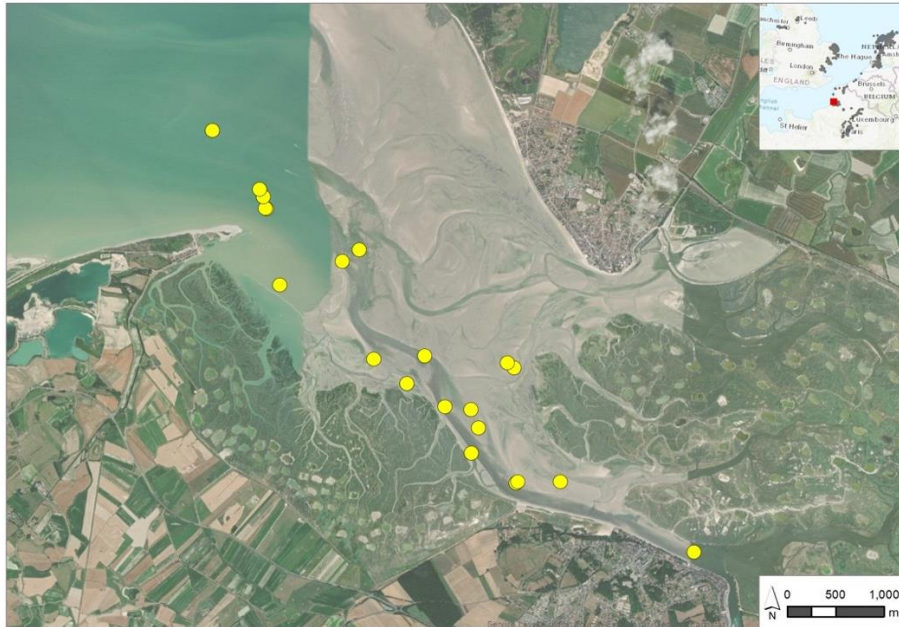


Figure 4. Distribution of GPS-fixes of eight Black-headed Gulls from The Netherlands on their wintering grounds per land use category. Land use is determined following Corine Land Cover 2018. Averages for all females, males and all birds combined are presented separately.

SUPPLEMENTARY MATERIAL

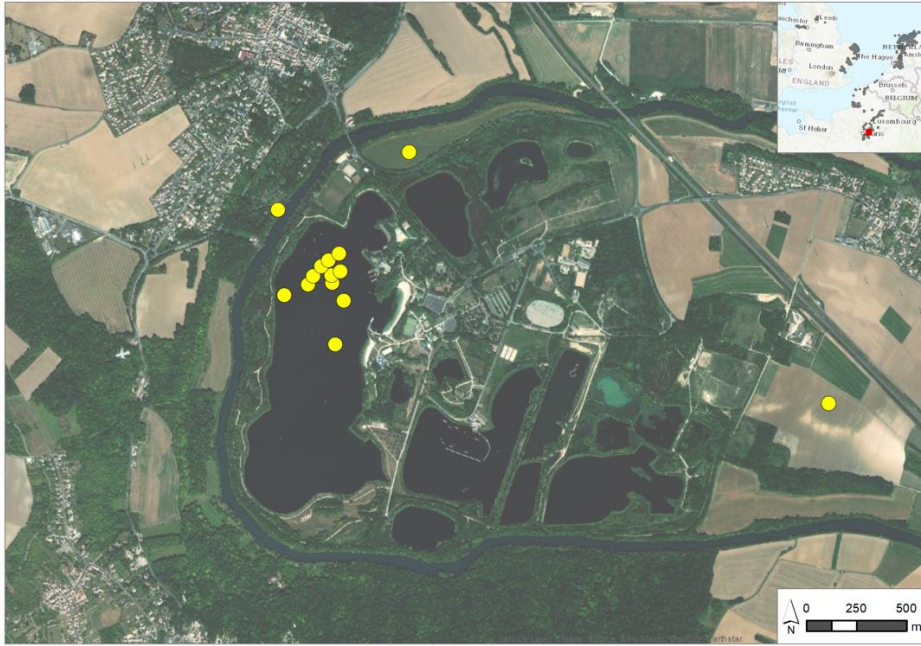
Examples of specific habitat types that Black-headed Gulls with GPS-loggers frequented during the winter.



Example of foraging behaviour in intertidal habitat



Example of residency in quarry



Example of sleeping on inland lakes



Example of residency in sewage water plant