Journal of Ornithology
https://doi.org/10.1007/s10336-023-02097-1

ORIGINAL ARTICLE

Habitat use across the tidal cycle by black-headed gulls breeding in the Wadden Sea

Rob S. A. van Bemmelen[1] · Sjoerd Duijns[1,4] · Laura L. Govers[2,3] · Ruben C. Fijn[1]

Received: 11 October 2021 / Revised: 11 July 2023 / Accepted: 1 August 2023

Abstract

Movements of birds foraging in intertidal areas are often strongly linked to the tidal cycle, as water levels determine where and when birds can forage. The strength of this link likely depends on the ability to forage in habitats other than intertidal areas and on constraints imposed by breeding duties. Few studies have focused on the use of intertidal areas by generalists, such as the black-headed gull *Chroicocephalus ridibundus*, that occupy a wide variety of habitats within and beside intertidal mudflats. We investigated to what degree black-headed gulls (1) use intertidal mudflats versus terrestrial habitats during different phases of the tidal cycle, (2) follow the tidal wave to exploit recently exposed mudflats and (3) whether these behaviours are influenced by central place foraging. For this, 11 black-headed gulls breeding on the Wadden Sea island Griend were tracked during two years using GPS loggers. When commuting to and from Griend, up to 75% of their time was spent in intertidal areas during low and incoming tide, which increased to 92% when not behaving as central place foragers. While their movements were strongly linked to the tidal cycle, they did not follow the tidal wave across the tidal basin during either period. Rather, individuals foraged either predominantly west or east of Griend during low and incoming tide and mostly remained visiting these areas when not behaving as central place foragers. As one of the most abundant species in the Wadden Sea, the extensive use of intertidal mudflats highlights the importance of black-headed gulls within the intertidal food web of the Wadden Sea.

Keywords *Chroicocephalus ridibundus* · Intertidal · Tidal wave · GPS-tracking

Zusammenfassung

Habitatnutzung von im Watt brütenden Lachmöwen während des Gezeitenzyklus

Die Ortsveränderungen von Vögeln, die in Gezeitenzonen Nahrung suchen, sind oft eng mit dem Gezeitenzyklus verbunden, da der Wasserstand bestimmt, wo und wann die Vögel auf Nahrungssuche gehen können. Wie stark diese Verbindung ist, hängt wahrscheinlich zum einen von der Fähigkeit ab, auch in anderen Lebensräumen als den Gezeitenzonen nach Nahrung zu suchen, zum anderen von den Einschränkungen, die sich aus den Anforderungen des Brütens ergeben. Es gibt nur wenige

Communicated by F. Bairlein.

✉ Rob S. A. van Bemmelen
rvanbemmelen@gmail.com

1 Waardenburg Ecology, Bird Ecology Group, Varkensmarkt 9, 4101 CK Culemborg, The Netherlands

2 Conservation Ecology Group, Groningen Institute for Evolutionary Life Sciences (GELIFES), University of Groningen, PO Box 11103, 9700 CC Groningen, The Netherlands

3 Department of Coastal Systems, NIOZ Royal Netherlands Institute for Sea Research, PO Box 59, 1790 AB Den Burg, The Netherlands

4 Present Address: Sovon Dutch Centre for Field Ornithology, Toernooiveld 1, 6525 ED Nijmegen, The Netherlands

Published online: 22 August 2023

Untersuchungen zur Nutzung von Gezeitenzonen durch Generalisten wie der Lachmöwe (*Chroicocephalus ridibundus*), die eine Vielzahl von Lebensräumen im und am Rande des Watts bewohnen. Wir untersuchten, wie intensiv Lachmöwen (1) während verschiedener Phasen des Gezeitenzyklus Wattflächen im Vergleich zu Flächen an Land nutzen, (2) der Ebbe folgen, um direkt vorher freigelegte Bereiche im Schlick zu nutzen, und (3) ob diese Verhaltensweisen von der Nahrungssuche an zentral gelegenen Stellen beeinflusst werden. Hierfür wurden 11 Lachmöwen, die auf der Wattenmeerinsel Griend brüten, zwei Jahre lang mit GPS-Loggern verfolgt. Auf dem Weg von und nach Griend verbrachten sie bei Ebbe und bei Flut bis zu 75% ihrer Zeit in Gezeitenzonen, was sich auf 92% erhöhte, wenn sie nicht an zentral gelegenen Plätzen Futter suchten. Zwar waren ihre Ortsveränderungen eng mit dem Gezeitenzyklus verknüpft, aber weder bei Ebbe, noch bei Flut folgten sie der Tide durch das Tidebecken. Stattdessen suchten die Tiere bei Ebbe und Flut überwiegend westlich oder östlich von Griend nach Nahrung und hielten sich meistens in diesen Gebieten auf. Als eine der häufigsten Arten im Wattenmeer unterstreicht die extensive Nutzung des Gezeitenschlicks die Bedeutung der Lachmöwe innerhalb des tideabhängigen Nahrungsnetzes des Wattenmeeres

Introduction

The habitats that animals select for foraging in relation to spatiotemporal changes in food availability are critical to their survival and reproduction (Manly et al. 2002). In intertidal areas, the tidal cycle creates regular but also highly fluctuating availability of foraging opportunities, which in turn drives bird movements. Species that feed exclusively on exposed intertidal mudflats, such as red knots *Calidris canutus*, are not able to forage during high tide and aggregate on high-tide roosts (van Gils et al. 2005). Species that utilize intertidal as well as other habitats, such as bar-tailed godwits *Limosa lapponica* during spring migration and Eurasian oystercatchers *Haematopus ostralegus*, forage on the mudflats during low tide and increase their potential foraging time by switching to alternative foraging habitats, such as inland coastal meadows or agricultural areas, during high tide (Caldow et al. 1999; Duijns et al. 2009; van der Kolk et al. 2020). Conceivably, movements of more generalist species that are less dependent for foraging on exposed mudflats may be less strongly linked to tidal cycles, as generalists may be able to continue foraging during high tide over flooded intertidal areas, for example, by foraging at the water surface or diving, or forage only opportunistically over intertidal areas.

Without animals moving, the time available for foraging on mudflats during a single tidal cycle would be dictated by the time the mudflats are exposed at that specific site. Because in large intertidal areas some mudflats become exposed earlier in the tidal cycle than others, birds can increase their foraging time by several hours by moving along the direction of the tidal wave; thus, starting in areas that become exposed first in the tidal cycle and then move with the receding waterline until areas become flooded again (van Gils et al. 2005; Granadeiro et al. 2006). The degree to which an individual moves along with the tidal wave may depend on its dependency on (recently exposed) intertidal mudflats for foraging and its ability to fully exploit foraging opportunities created by the movement of the tidal wave. For example, central place foragers that need to return regularly to their nesting site may be constrained in tracking the tidal wave to maximize foraging time because the most optimal frequency and duration of foraging trips may not match the rhythm of the tidal cycle or allow visiting areas at larger distances from the colony (Orians and Pearson 1979). Consequently, breeding individuals of species that rely heavily on intertidal mudflats for foraging are expected to time their foraging trips to maximize their use of intertidal mudflats, whereas species less dependent on exposed mudflats may time their foraging trips largely irrespective of the tidal cycle. When birds are constrained to follow the tidal cycle by breeding, birds are expected to increase their time spent at exposed mudflats and align their movements with the tidal wave when breeding duties are lifted.

In the Wadden Sea, the largest connected intertidal flat system in the world, the link between movements and the tidal cycle has been especially well-studied during the non-breeding period in a few specialist foragers on bivalves and polychaetes with strong dependency on intertidal mudflats for foraging. Habitat selection in the Wadden Sea has been especially well-studied in waders, in particular red knot *Calidris canutus* (van Gils et al. 2005; Bijleveld et al. 2016), bar-tailed godwit *Limosa lapponica* (Duijns et al. 2015) and Eurasian oystercatcher *Haematopus ostralegus* (Ens et al. 2014; van der Kolk et al. 2020). These species vary in the extent to which they are dependent for foraging on (exposed) intertidal mudflats and share the intertidal mudflats of the Wadden Sea with many species that may be less specialized in foraging in this habitat. These more generalist species may be abundant and therefore likely an important component of the intertidal food web, to what degree their movements are driven by the tidal cycle and the need to regularly return to the breeding colony, has been poorly studied.

We studied the movements of the black-headed gull *Chroicocephalus ridibundus*, one of the most abundant bird species in the Dutch Wadden Sea (Roomen et al. (2020), www.stats.sovon.nl). In accordance with its broad diet (Cramp and Simmons 1983), the black-headed gull is known to forage in a wide variety of habitats found within the Wadden

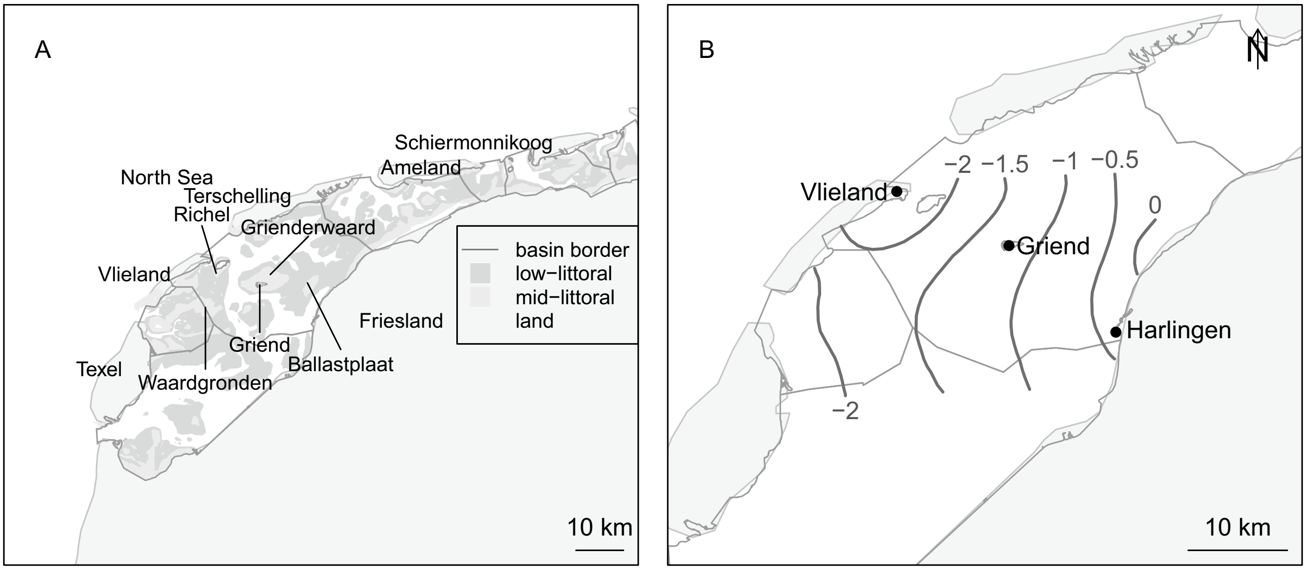

Fig. 1 **a** The Dutch Wadden Sea with the names of islands, uninhabited islands and intertidal areas mentioned in the main text. Black-headed gulls were tracked from the island of Griend. Delineation of low- and mid-littoral and basins are based on Baptist et al. (2019). **b** Progression of the tidal cycle from west to east across the main part of the study area, the Vlie basin, redrawn from van Gils et al (2005)

Sea, such as exposed mudflats, shallow water, gullies and salt marsh areas (van de Kam et al. 1999; Horn et al. 2020), but also in a wide variety of habitats occurring outside the intertidal area, such as agricultural or urban areas (Maciusik et al. 2010). Here, we studied how the use of intertidal versus terrestrial (mainland or Griend itself) areas varies during the tidal cycle, to what extent they synchronize their movements with the tidal cycle, and whether central place foraging affects these behaviours. By using GPS-tracking devices, we studied the movements of 11 individual black-headed gulls breeding on Griend, an uninhabited island in the Dutch Wadden Sea (Fig. 1a), during two consecutive breeding seasons. These black-headed gulls have access to the intertidal mudflats directly surrounding the island of Griend, as well as intertidal mudflats and agricultural areas further from the colony. Griend is positioned in the centre of the Vlie tidal basin, wherein mudflats in the west become exposed around two hours earlier than those in the east (Fig. 1b). Thus, black-headed gulls aiming to forage on exposed mudflats may start foraging early in the cycle in the west, and then proceed to the east to fully exploit the potential foraging time. During high tide, they have limited access to exposed mudflats and therefore may roost or forage on land (either in the colony at Griend or elsewhere), or forage over flooded mudflats and gullies. We expect that breeding duties limit the ability to track the tidal wave, and therefore more closely follow the tidal wave and increase their time spent at the intertidal flats during low tide when relieved from breeding duties. As tracking studies of gulls and related species have highlighted strong individuality in movement patterns (Phillips et al. 2017; Borrmann et al. 2019; van Donk et al. 2020), we also studied to what extent individuals keep visiting the same areas during low and high tide when relieved from breeding duties.

Methods

Study area

Griend (53.25°N, 5.25°E) is an uninhabited island in the Dutch Wadden Sea, where the tidal cycle imposes a *ca* 12.5 h cycle of availability of mudflats. Griend is positioned in the centre of the Vlie tidal basin, which stretches from Vlieland in the west to the mainland in the east (Fig. 1). The black-headed gull colony at Griend is the largest colony in the Netherlands, although it has declined from 35,000 pairs in 2008 to fewer than 15,000 pairs in 2019 (Majoor 2018; Govers and Reijers 2021).

GPS-tracking

On 19 May 2019, 11 breeding black-headed gulls were captured in the colony (14,609 breeding pairs in 2019) at the island of Griend (65 ha, Govers and Reijers (2021); Fig. 1). Birds were captured on the nest using a clap-net or walk-in trap approximately one and a half weeks before eggs would hatch (based on observations of settling birds by the local wardens). Birds were colour-ringed and fitted with a GPS logger (Ecotone, model PICA, ~ 4.5 gr, solar-powered, L:35 × W:15 × H:10 mm) using a backpack loop harness constructed from Teflon (Kenward 1985). The added

Table 1 Number positions and number of days with positional data, after regularization of GPS-fixes to hourly intervals, of 11 black-headed gulls tagged at Griend

	2019				2020			
	CPF		non-CPF		CPF		non-CPF	
bird id	*n* pos	*n* days	*n* pos	*n* days	*n* pos	*n* days	*n* pos	*n* days
A	150	25	820	96	686	63	342	63
B	282	27	483	51	185	46	498	46
C	496	45	769	74	971	83	900	83
D	286	26	37	3	731	61	120	61
E	0	0	198	19	0	0	0	0
F	467	36	2	1	852	87	147	87
G	566	47	833	82	44	7	242	7
H	523	39	26	2	770	69	21	69
I	63	6	234	21	0	0	0	0
J	120	24	579	91	644	54	610	54
K	429	34	1,174	104	925	80	155	80

CPF indicates the period when gulls behaved as central place foragers

weight of the logger, harness and rings amounted to 6.3 g, representing less than 3% of the body mass of all birds (average body mass of 242 g ± 16.4 SD, range: 220–270 g), to a maximum of 2.9% in the lightest bird (body mass of 220 g). Handling time between capture and release was between 10 and 20 min per bird.

GPS loggers stored positional data on internal memory and relayed this data to a base station positioned in the colony. Whenever loggers were within a range of 200–500 m from the base station, loggers were recorded as 'in range' by the base station and stopped taking positions to reduce battery drainage. The internal batteries of the loggers were charged by a solar panel. To balance the risk of draining the batteries and maximizing the detail of the GPS-data, we varied the settings of the loggers in 2019, and in 2020 setting were changed again (Supplementary Fig. S1). Settings varied in the interval between GPS-fixes from 10 to 60 min and whether they were active 24 h per day or only between 6:00 and 18:00 local time. Data were regularized to equal time intervals of 60 min to retain data from all individuals, using the redisltraj function from the adehabitat package in R (Calenge 2006).

From the 11 individual black-headed gulls that were tracked during the breeding season in 2019, 9 individuals were also tracked in 2020 (Table 1). Bird G was last recorded at Griend on 25 May 2020 and found dead at Vlieland in 2021. The fate of the two individuals missing in 2020 is unknown.

For the purpose of this study, we only included data from the period when they were using the Wadden Sea and therefore the migration and wintering periods were excluded from the analysis (see Fijn et al. 2022 for details on migration and wintering behaviour). The first full day of tracking data was excluded to reduce potential effects of catching. To compare habitat use when the birds behaved as central place foragers with the time they did not, we defined periods of central place foraging from Griend based on the observed pattern of visits to the vegetated part of the island. The first of three consecutive days with visits to Griend was taken as the start of central place foraging from Griend. The first day before three consecutive days with no visits to Griend was assigned as the end of central place foraging behaviour. In between these days, an individual could occasionally not be recorded at Griend, but this constituted usually only a single day (Fig. 2). Individual K did however have a 6-day absence from Griend (Fig. 2), which was excluded from the central place foraging period. Because we had only very limited observational data on the status of most nests of tagged individuals and only for the breeding season in 2019, it was impossible to divide the data into stereotypical periods of the breeding cycle (e.g. incubation, chick-rearing, etc.).

Outside the periods of central place foraging, we identified days on which birds visited the Vlie tidal basin (Fig. 2). Data from these days were used when comparing habitat use and movements during the tidal cycle between periods of central place foraging and outside these periods.

Tracking the tidal wave

To identify whether black-headed gulls behaving as central place foragers move with the tidal wave to exploit recently exposed mudflats, we studied whether they moved westwards earlier during the tidal cycle than eastwards and undertook longer trips earlier after high tide. We only used complete foraging trips, i.e. trips starting and ending at the colony. For the start and end of each trip, the time difference relative to the nearest high tide at Harlingen was calculated.

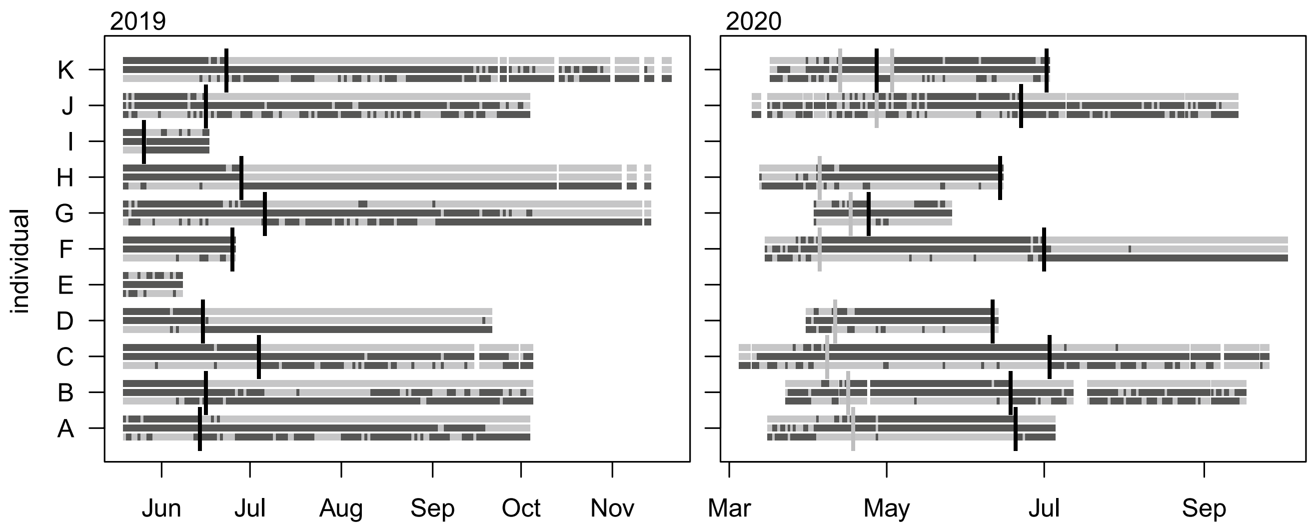

Fig. 2 Daily presence (black) and absence (grey) of positions on Griend (upper lines), in the Vlie basin (middle lines) and elsewhere (lower lines) per individual black-headed gull tracked from Griend; gaps indicate missing data. Vertical lines show the start (dark grey; 2020 only) and end (black; both years) of central place foraging periods from Griend. In bird K in 2020, a 6-day period during which the bird did not visit Griend during is categorized as not central place foraging. Note the difference in x-axis scales between the years

For both periods (central place foragers or not), we calculated the distance to the colony (53.251°N 5.2511°E), with negative values for positions west of Griend, and related this to the time relative to high tide in Harlingen. It was predicted that birds would move from west of Griend to east of Griend during a tidal cycle. In addition, we calculated the proportion of tidal cycles in which positions further than 1 km from the colony were all west, all east or in both directions from Griend. If birds track the tidal wave across the entire basin, a substantial proportion of tidal cycles would have positions in both directions from Griend.

Time spent in habitats

We categorized each position in the regularized GPS data into four habitats: (1) The vegetated part of the island Griend, (2) the intertidal area of the Wadden Sea, (3) land other than Griend (either the mainland or the other Wadden Sea islands) and (4) North Sea. Tidal data were not available for Griend. Griend is positioned in the centre of a tidal basin (Vlie), between the tidal channel between the islands Vlieland and Terschelling (*ca.* 12 km NW of Griend) and the Frisian coast (Harlingen is located *ca.* 13.5 km SE of Griend). The tidal data for Harlingen were downloaded (https://waterinfo.rws.nl) and used to represent the tidal cycle for foraging conditions at mudflats. Habitat use was quantified as the proportion of daily positions in each habitat. Per day, the number of positions within each habitat versus the number of positions in other habitats were used as the response in a binomial generalized linear mixed model (GLMM), with period (two levels; either CPF or non-CPF), tidal cycle phase (hourly levels) and their interaction, as fixed effects, and random intercepts per individual and year. Models were fitted using R-INLA (Rydell et al. 2010). The sample size for the analysis of the time spent in each habitat as a function of the tidal cycle is shown in Table 1.

Individuality in area use

The individual fidelity to areas during high or outgoing tide and low or incoming tide during and outside periods of central place foraging was quantified. First, a 95% utilization density (UD) kernel was estimated for each individual per period, with the smoothing factor estimated using the LSCV method, assuming a bivariate normal kernel and using the adehabitat package in (Calenge et al. 2014). Then, the degree to which individuals used the same areas in different periods, and the overlap in area use of different individuals within each period, were quantified as the Bhattacharyya's affinity (BA) index, a measure of overlap of kernels (Toohey 2015; Cleasby et al. 2019). Differences were assessed by 10,000 randomizations to create a null distribution against, which the observed values were compared.

All calculations were performed in R version 4.2.2 (2022-10-31) (R Core Team 2022).

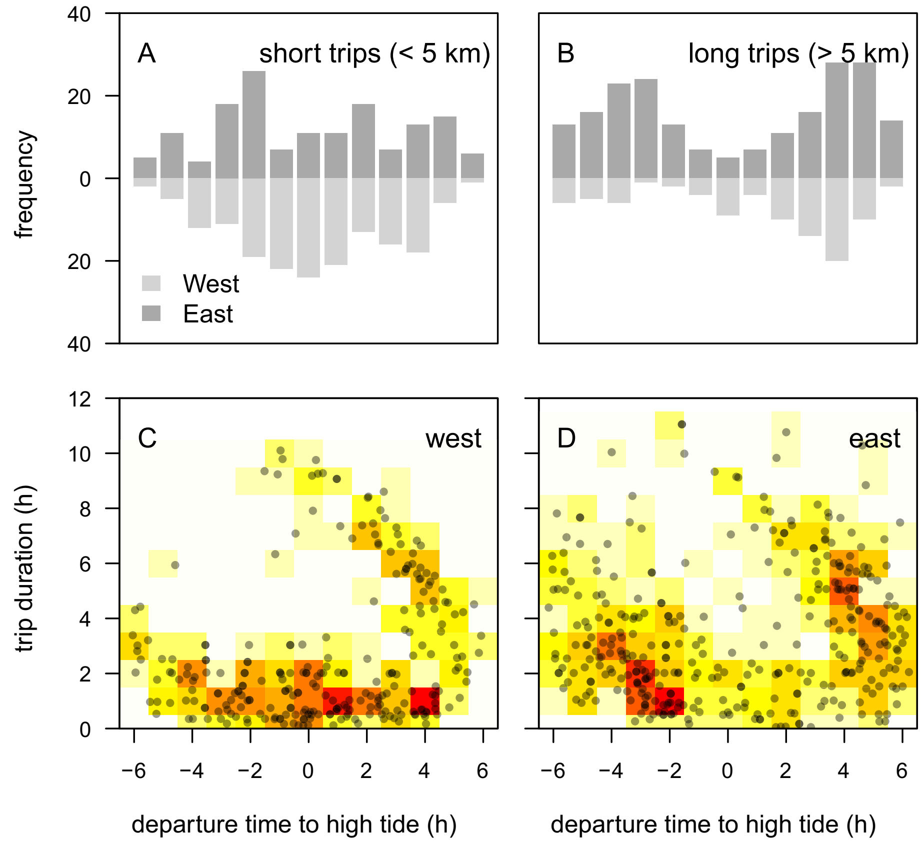

Fig. 3 Duration and timing of 620 foraging trips of 11 black-headed gulls from the colony at Griend relative to the time of high tide at Harlingen. Frequency distribution of the timing of departure from the colony for westward (light grey) and eastward (dark grey) trips of **a** less than 5 km, staying largely within the Grienderwaard, and **b** further than 5 km, venturing outside the Grienderwaard. Relation between the timing of departure from the colony and the duration of foraging trips, for westward **c** and eastward **d** trips

Results

Timing of foraging trips in the tidal cycle

During the central place foraging periods, the duration of both westward and eastward foraging trips varied roughly between one and eight hours (Fig. 3c, d, Supplementary Fig. S2). During longer foraging trips, black-headed gulls generally went further from the colony (Supplementary Fig. S2). The slope of this relation among westward trips was slightly steeper than that among eastward trips ($\beta = -0.235$, 95% CrI = − 0.564–0.094). Trips where birds stayed within 5 km of the colony, thus within the Grienderwaard, were initiated (Fig. 3a) or finished (Supplementary Fig. S3a) at any part of the tidal cycle and generally lasted less than 3 h. However, while the initiation of short eastward trips was rather evenly across the tidal cycle, westward trips were mostly initiated during high or outgoing tide.

Longer trips, venturing further than > 5 km and thus outside the Grienderwaard, were more common among eastward trips. These trips were also initiated during any part of the tidal cycle, but substantially less often in the hours around high tide at Harlingen. This pattern was largely similar between westward and eastward trips, with no indication that westward trips were initiated earlier after high tide, but with eastward trips more commonly initiated during incoming tide (Fig. 3b). Among trips longer than about 3 h, trips were shorter when initiated later after high tide, with trips of up to 10 h around high tide and short trips initiated during upcoming tide. This was true for both westward and eastward trips, but more variable among eastward trips (Fig. 3c, d). The far majority of westward trips venturing outside the Grienderwaard finished around two hours before high tide (Supplementary Fig. S3b, c), whereas eastward trips finished mostly during a broader time frame, from about two hours before high tide to high tide (Supplementary Fig. S3b, d).

Tracking of the tidal wave

During the periods of central place foraging, black-headed gulls mostly ventured into western or eastern direction from the breeding colony on Griend, with birds spending most time in the intertidal areas South of Vlieland (Waardgronden), around Griend (Grienderwaard) and Ballastplaat (for topography, see Fig. 1). Most foraging trips to intertidal areas stayed within *ca.* 10 km to the west (Waardgronden, Richel) or *ca.* 10 km east (Ballastplaat) of Griend (Fig. 4a). During high tide, they mostly stayed on Griend, or moved to the Frisian coast or to the Wadden Sea isles further from the colony (Fig. 4a, c). Individuals

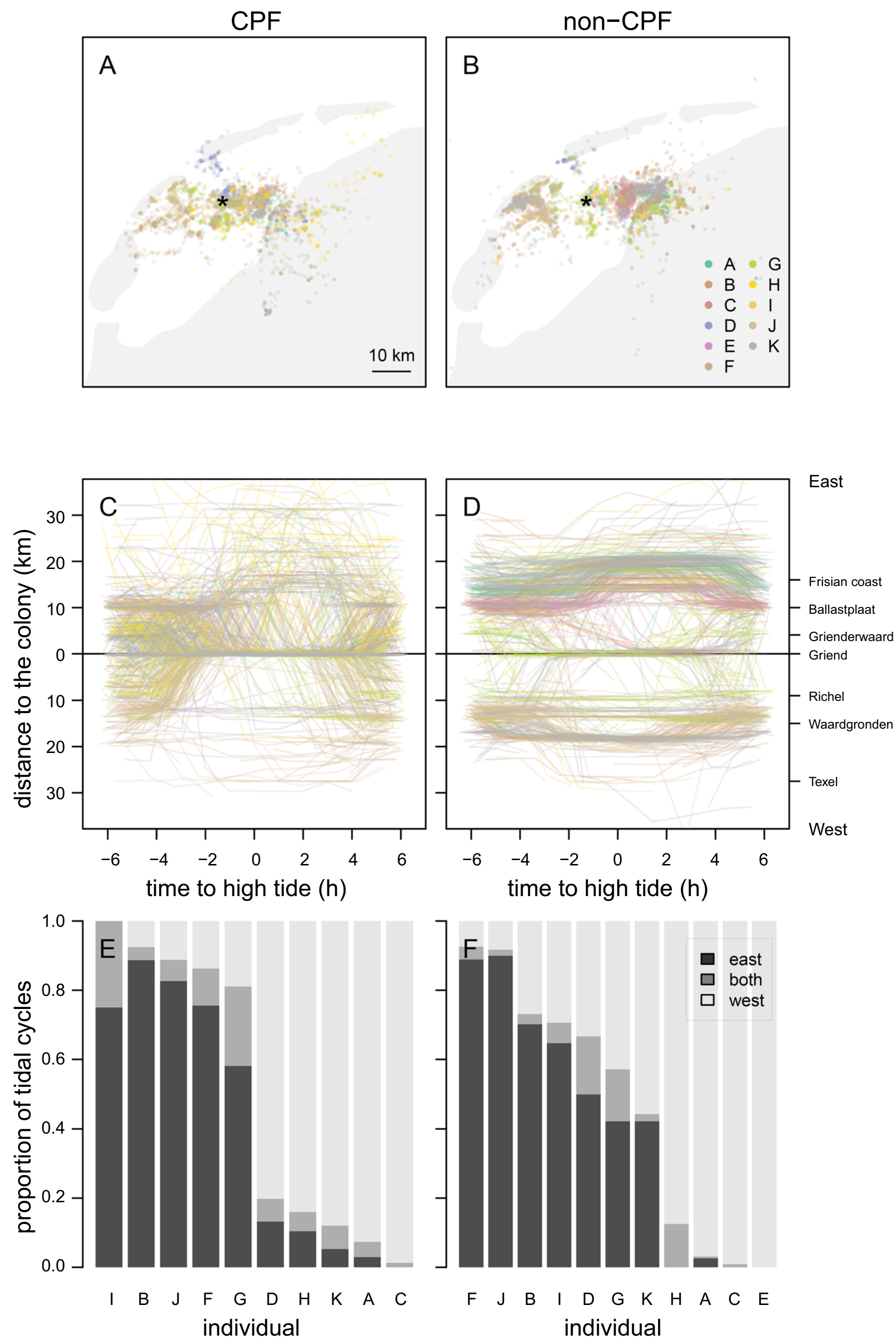

Fig. 4 Distribution of 11 black-headed gulls (A-K) during **a** periods of central place foraging from Griend ($n = 9190$ positions, 2086 tidal cycles) and **b** outside this period ($n = 8190$ positions, 1650 tidal cycles) in 2019–2020. Distance to the colony at Griend relative to the time of high tide at Harlingen when moving west (below the horizontal line) or east (above the horizontal line), when central place foraging **c** or not **d**. Highlighted on the right side of d and f are the most important areas, of which the topography can be found in Fig. 1. In **e** and **f**, showing the proportion of tidal cycles with positions all west of Griend, all east of Griend, or both, with individuals ranked to the proportion of tidal cycles east of Griend. Note that individual E does not occur in plot e

had a strong tendency to predominantly move east ($n = 5$) or west ($n = 5$), with positions in both directions during only a minority of tidal cycles (1 to 25%; Fig. 4e).

This pattern inversed when not central place foraging. During that period, black-headed gulls spent high tide mostly on the mainland or Vlieland and ventured during low tide to nearby intertidal areas (Waardgronden, Ballastplaat), but must less to the Grienderwaard (Fig. 4b, d). The tendency of individuals to predominantly move either west or east from Griend was somewhat attenuated, although still two individuals predominantly moved east and four west of Griend. The proportion of cycles with positions in both directions remained very low (0 to 17%; Fig. 4f).

Time spent in habitats

The tidal cycle had a large effect on habitat use of black-headed gulls (Fig. 5. In the periods of central place foraging, black-headed gulls spent high and outgoing up to 69% of their time on Griend, while the proportion of time spent

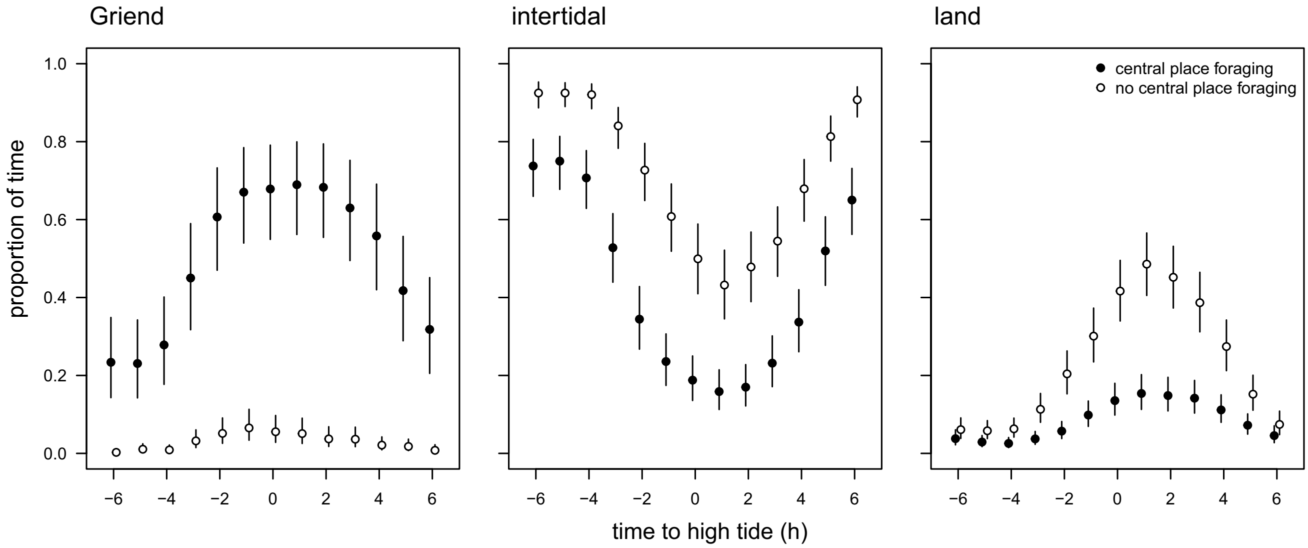

Fig. 5 Proportion of time spent by 11 black-headed gulls in three habitats as a function of tidal cycle at Harlingen (x-axis), during the periods in 2019–2020 when they were central place foragers from Griend (dots; $n = 8542$ tracking days, 11 individuals) and outside these periods but when they were using the same tidal basin (open circles; $n = 7769$ tracking days, 10 individuals). The three habitats: **a** Griend, including the colony, **b** intertidal areas and c) land other than Griend. Error bars are 95% credible intervals. Dots represent median and error bars 95% credible intervals of the posterior distributions. See Table 1 for details on sample size

on intertidal flats decreased to 16% on intertidal flats and proportion of time on land other than Griend peaked at 15%. This changed during low and incoming tide, when they spent, respectively down to 23% of their time on Griend, up to 75% on intertidal flats and down to 3% on land other than Griend.

Outside the periods of central place foraging, black-headed gulls strongly reduced their time on Griend to at most 7% of their time. The time spent on land elsewhere increased up to 49% 2 h after high tide. The time spent in the intertidal zone increased up to 92% during 5 to 3 h before high tide.

All contrasts between the parameters of periods had 95% of the posterior distributions far from zero, indicating a strong effect of central place foraging on the time spent in the three habitat types.

Individuality in area use

Overlap between kernels between the two periods was similar between and within individuals during high/outgoing tide ($p = 0.054$), but overlap was substantially larger within than between individuals during low/incoming tide ($p < 0.001$, Supplementary Fig. S4). The distribution of BA values within individuals between periods during low/incoming tide, ranging from 0.24 to 0.74, indicates that individuals used at least part, but often a substantial part of the same areas during low/incoming tide.

Discussion

Although black-headed gulls are known to forage in a wide variety of habitats (Maciusik et al. 2010; Horn et al. 2020), the individuals tracked in our study spent a large portion of their time on intertidal mudflats surrounding their breeding colony at Griend, in the Dutch Wadden Sea, indicating the importance of the intertidal habitat for this species. Their movements were largely aligned with the rhythm of the tidal cycle, as expressed through correlations of habitat use, departure and arrival to the colony and distance to the colony with phase of the tidal cycle. Although the use of intertidal mudflats of the Wadden Sea by black-headed gulls has been recognized (van de Kam et al. 1999), our study is the first to describe this in detail at the level of individuals.

During low and incoming tide ánd commuting to and from Griend, black-headed gulls spent around 53–67% of their time at intertidal mudflats, in particular in mid- to low-littoral areas—mudflats that are exposed at that time. The extensive use of exposed mudflats was expected considering observations from Griend indicating that their diet consists for *ca* 90% of crustaceans and polychaetes, which are prey that typically occur at intertidal mudflats, and only occasionally of terrestrial prey (Dijk and Oosterhuis (2010), Oosterhuis and Heideveld (2000), Date Lutterop and René Oosterhuis *in litt*). A diet dominated by crustaceans and polychaetes was also found in intertidal areas in Scotland (Curtis et al. 1985). These are prey types that are mostly available when mudflats are exposed.

The considerable use of intertidal areas around high tide, especially when not commuting to and from Griend, suggests that black-headed gulls may also continue foraging here, despite these areas being flooded at that time. Indeed, black-headed gulls are known to surface peck while swimming over recently flooded mudflats (van de Kam et al. (1999); *pers obs*). In gullies, they may also profit from discards from shrimp fisheries, like herring gulls *Larus argentatus* (Camphuysen et al. 2015). Unfortunately, these types of fine-scale behaviour could not be inferred from our GPS-data. In contrast to flooded mudflats and terrestrial habitats such as agricultural fields, black-headed gulls seem to have less feeding opportunities in the colony. The apparent lack of opportunities for self-foraging in or near the colony may explain why incidences of kleptoparasitism of black-headed gulls on Sandwich terns *Thalasseus sandvicensis* at the colony peak just before and around high tide (Stienen et al. 2001), and why Griend was only occasionally visited outside the periods of central place foraging.

Movements of black-headed gulls from Griend showed a clear relation to the tidal cycle, in accordance with earlier studies (Curtis and Thompson 1985; Schwemmer and Garthe 2008). During the outgoing tide, birds moved to mudflats both west and east from the colony, whereas during the incoming tide, birds moved either back to the colony or to the mainland. The predominance of colony departure in the hours after high tide and arrivals before high tide corroborate the findings of Schwemmer and Garthe (2008), who also found movements between marine areas and a black-headed gull colony in the German Wadden Sea to drop at high tide. Contrary to expectations, we did not find evidence of black-headed gulls following the tidal wave from west to east across the Vlie basin, as has been shown for red knots (van Gils et al. 2005). In waders such as the red knot, bar-tailed godwit and avocet *Recurvirostra avosetta*, individuals follow the water line during the tidal cycle to forage in recently exposed mudflats (van Gils et al. 2005; Granadeiro et al. 2006; Duijns and Piersma 2014). Red knots require a wet sediment to optimally detect bivalve prey using sensory organs in their bill tip (Piersma et al. 1998). Gulls do not possess such sensory organs in their bill tip and may therefore be less dependent on wet sediments for efficient foraging; they may be able to forage in both drier sediments and wetter (flooded) conditions. Indeed, with an average of 3.3 h, duration of foraging trips from Griend was substantially shorter than the tidal cycle of about 12.5 h, indicating they did not extent their foraging time to the full potential. In addition, for longer trips, black-headed gulls departed from and returned to Griend at the same time relative to high tide, apparently not exploiting the earlier exposure of the westernmost mudflats—although they did seem to exploit the earlier exposure of the mudflats directly west of Griend. Finally, individuals rarely used areas west and east of Griend within the same tidal cycle. These observations suggest that black-headed gulls were constraint to track the tidal wave throughout an entire tidal cycle due to central place foraging, chick provisioning and/or partitioning of incubation and chick guarding roles between partners. However, black-headed gulls still did not track the tidal wave when relieved from breeding duties, suggesting any energetic or time constraints imposed by central place foraging may be similar across a longer period. Alternatively, the combination of foraging in agricultural areas (where they probably feed predominantly on earthworms) during high tide and switch to nearby intertidal mudflats are exposed may render a more profitable foraging strategy than traveling several tens of kilometres with the tidal wave across the tidal basin and feed predominantly on crustaceans and polychaetes.

Instead of using the entire the Vlie basin, the 11 black-headed gulls tracked in our study showed strong individuality in area selection, both when commuting to and from Griend and when not. Such individuality in foraging area selection seems the rule among gull species, such as great black-backed gull *Larus marinus* and European herring gull (Borrmann et al. 2019; van Donk et al. 2020) and seabirds in general (Phillips et al. 2017). Consistency in foraging site selection may be beneficial when environments are predictable, and individuals can forage more efficiently (Irons 1998). However, specializing on exposed mudflats that are available for only a short time per tidal cycle will limit the potential foraging time. Individual variation in time constraints can ultimately affect survival, as has been shown for Eurasian oystercatchers (van der Kolk et al. 2021). Given their flexibility in foraging behaviour, black-headed gulls may be able to compensate for limited foraging time at mudflats by foraging in other habitats and tidal phases.

Our study shows that, despite being considered a habitat and food generalist at the species level, black-headed gulls breeding at Griend make extensive use of the intertidal habitats of the Wadden Sea, thereby strongly responding to the tidal cycle much like waders do, albeit with the flexibility to forage over open water or in terrestrial habitats. With ca. 15,000 pairs of black-headed gulls breeding on Griend alone (Govers and Reijers 2021), several 1000 s breeding elsewhere in the Wadden Sea, and many 10,000 s more migrating through or wintering in the Wadden Sea (Roomen et al. (2020); www.stats.sovon.nl), the species is one of the most numerous waterbirds in the area and therefore likely an important consumer of macrobenthos. With even basic ecological data lacking, there is ample potential for future studies on black-headed gulls and their role in the food web of the Wadden Sea ecosystem and beyond.

Acknowledgements Tracking black-headed gulls was commissioned by Groningen University (RUG) and executed by Bureau Waardenburg (BW) as part of the monitoring program into effects of the habitat restoration activities of Griend. The loggers were financed by the 'Griend Research Project', funded by Waddenfonds and Rijkswaterstaat. Laura Govers was also funded by NWO VENI 0.16.VENI.181.087. The fieldwork was performed under a project license for animal procedures AVD401002015102 of the Central Authority for Scientific Procedures on Animals. We thank Han Olff and Nadia Hijner (RUG), who provided guidance to another analysis of the data by Shuiqing He (RUG), and thereby contributed to the directions of the analyses presented here. We also thank Elisa Bravo Rebolledo (BW), Date Lutterop and Giny Kasemir for help in the field. Fieldwork was carried in nature reserves of Natuurmonumenten (NM). Many thanks to Quirin Smeele of NM for his cooperation and hospitality during meetings. We thank the two anonymous reviewers for their time and input, that improved our manuscript.

Data availability The tracking data is available at www.movebank.org under the study ID 2891840215.

Declarations

Conflict of interest The authors declare no conflict of interest.

References

Bijleveld AI, MacCurdy RB, Chan Y-C et al (2016) Understanding spatial distributions: Negative density-dependence in prey causes predators to trade-off prey quantity with quality. Proce Royal Society B Biol Sci 283:20151557. https://doi.org/10.1098/rspb.2015.1557

Borrmann RM, Phillips RA, Clay TA, Garthe S (2019) High foraging site fidelity and spatial segregation among individual great black-backed gulls. J Avian Biol 50:12

Baptist MJ, van der Wal JT, Folmer EO, Gräwe U, Elschot K (2019) An ecotope map of the trilateral Wadden Sea. J Sea Res 152:101761. https://doi.org/10.1016/j.seares.2019.05.003

Caldow RWG, Goss-Custard JD, Stillman RA et al (1999) Individual variation in the competitive ability of interference-prone foragers: The relative importance of foraging efficiency and susceptibility to interference. J Ani Ecol 68:869–878. https://doi.org/10.1046/j.1365-2656.1999.00334.x

Calenge C (2006) The package "adehabitat" for the R software: A tool for the analysis of space and habitat use by animals. Ecol Modell 197:516–519. https://doi.org/10.1016/j.ecolmodel.2006.03.017

Calenge C, Dray S, Royer M (2014) Package 'adehabitatLT'

Camphuysen KC, Shamoun-Baranes J, Van Loon EE, Bouten W (2015) Sexually distinct foraging strategies in an omnivorous seabird. Mar Biol 162:1417–1428

Cleasby IR, Wakefield ED, Morrissey BJ et al (2019) Using time-series similarity measures to compare animal movement trajectories in ecology. Behav Ecol Sociobiol 73:151. https://doi.org/10.1007/s00265-019-2761-1

Cramp S, Simmons KEL (1983) Handbook of the birds of europe, the middle east and north africa. In: Cramp S (ed) The birds of the western palearctic, waders to gulls. Oxford University Press, Oxford

Curtis DJ, Thompson DB (1985) Spacing and foraging behaviour of black-headed gulls larus ridibundus in an estuary. Ornis Scand 11:245–252

Curtis D, Galbraith C, Smyth J, Thompson D (1985) Seasonal variations in prey selection by estuarine black-headed gulls (larus ridibundus). Estuar Coast Shelf Sci 21:75–90

Duijns S, Piersma T (2014) Interference competition in a sexually dimorphic shorebird: Prey behaviour explains intraspecific competition. Ani Behav 92:195–201. https://doi.org/10.1016/j.anbehav.2014.04.007

Duijns S, van Dijk JGB, Spaans B et al (2009) Foraging site selection of two subspecies of bar-tailed godwit *Limosa lapponica* : Time minimizers accept greater predation danger than energy minimizers. Ardea 97:51–59. https://doi.org/10.5253/078.097.0107

Duijns S, Knot IE, Piersma T, van Gils JA (2015) Field measurements give biased estimates of functional response parameters, but help explain foraging distributions. J Ani Ecol 84:565–575. https://doi.org/10.1111/1365-2656.12309

Ens B, Bom RA, Dokter AM et al (2014) Nieuwe ontdekkingen en mogelijkheden in het onderzoek aan Scholeksters dankzij het UvA Bird Tracking Systeem. Limosa 87:117–128

Fijn RC, Govers LL, Lutterop D et al (2022) Evidence of nocturnal migration over sea and sex-specific migration distance of Dutch black-headed gulls. Ardea 110:15–29. https://doi.org/10.5253/arde.v110i1.a8

Govers L, Reijers VC (2021) Griend: Een bewogen eiland. KNNV Uitgeverij

Granadeiro JP, Dias MP, Martins RC, Palmeirim JM (2006) Variation in numbers and behaviour of waders during the tidal cycle: Implications for the use of estuarine sediment flats. Acta Oecologica 29:293–300

Horn S, Schwemmer P, Mercker M et al (2020) Species composition of foraging birds in association with benthic fauna in four intertidal habitats of the wadden sea. Estuarine Coast Shelf Sci 233:106537. https://doi.org/10.1016/j.ecss.2019.106537

Irons DB (1998) Foraging area fidelity of individual seabirds in relation to tidal cycles and flock feeding. Ecology 79:647–655

Kenward RE (1985) Raptor radio-tracking and telemetry. ICBP Tech Publ 5:409–420

Maciusik B, Magdalena L, Skórka P (2010) Corridors, local food resources, and climatic conditions affect the utilisation of the urban environment by the black-headed gull larus ridibundus in winter. Ecol Res 25:263–272

Majoor F (2018) Kokmeeuw chroicocephalus ridibundus. Vogelatlas van Nederland. Kosmos Uitgevers, Utrecht/Antwerpen, pp 288–289

Manly BF, McDonald L, Thomas D et al (2002) Resource selection by animals. Springer, New York

Oosterhuis R, Heideveld S (2000) Griend, vogels en bewaking 2000. Vereniging Natuurmonumenten, Arnhem

Orians GH, Pearson NE (1979) On the theory of central place foraging. In: Horn DJ, Mitchell RD, Stairs GR (eds) Analysis of ecological systems. Ohio State University Press, Ohio, USA, pp 154–177

Phillips RA, Lewis S, González-Solis J, Daunt F (2017) Causes and consequences of individual variability and specialization in foraging and migration strategies of seabirds. Marine Ecol Prog Ser 578:117–150

Piersma T, van Aelst R, Kurk K et al (1998) A new pressure sensory mechanism for prey detection in birds: The use of principles of seabed dynamics? Proce Royal Soci London Series b: Biol Sci 265:1377–1383. https://doi.org/10.1098/rspb.1998.0445

R Core Team (2022) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria

Rydell J, Bach L, Dubourg-Savage M-J et al (2010) Bat mortality at wind turbines in northwestern europe. Acta Chiropterologica 12:261–274. https://doi.org/10.3161/150811010x537846

Schwemmer P, Garthe S (2008) Regular habitat switch as an important feeding strategy of an opportunistic seabird species at the interface between land and sea. Estuarine Coast Shelf Sci 77:12–22. https://doi.org/10.1016/j.ecss.2007.08.017

Stienen EWM, Brenninkmeijer A, Geschiere CE (2001) Living with gulls: The consequences for sandwich terns of breeding in association with black-headed gulls. Waterbirds 24:68–82

Toohey K (2015) SimilarityMeasures: Trajectory Similarity Measures

van de Kam J, Ens BJ, Piersma T, Leo Z (1999) Ecologische atlas van de nederlandse wadvogels. Schuyt & Co, Haarlem

van der Kolk H-J, Ens BJ, Oosterbeek K et al (2020) Shorebird feeding specialists differ in how environmental conditions alter their foraging time. Behav Ecol 31:371–382. https://doi.org/10.1093/beheco/arz189

van der Kolk H-J, Ens BJ, Frauendorf M et al (2021) Why time-limited individuals can make populations more vulnerable to disturbance. Oikos 130:637–651

van Dijk K, Oosterhuis R (2010) Herkomst, aantallen en broedsucces van kokmeeuwen op griend. Limosa 83:21–35

van Donk S, Shamoun-Baranes J, Bouten W et al (2020) Individual differences in foraging site fidelity are not related to time-activity budgets in herring gulls. Ibis 162:429–445

van Gils JA, Dekinga A, Spaans B et al (2005) Digestive bottleneck affects foraging decisions in red knots *Calidris canutus* II. Patch choice and length of working day: *Patch choice under a digestive constraint*. J Ani Ecol 74:120–130. https://doi.org/10.1111/j.1365-2656.2004.00904.x

van Roomen M, Agblonon G, Langendoen T et al (2020) Simultaneous january 2020 waterbird census along the east atlantic flyway: National reports. In: Roomen M (ed) Wadden Sea Flyway Initiative p/a Common Wadden Sea Secretariat. Wilhelmshaven; Germany; Wetlands International; Wageningen; The Netherlands; BirdLife International; Cambridge; United Kingdom