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Original Article

Individual specialization on fishery discards by lesser black-backed gulls (*Larus fuscus*)

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While seabird–fishery associations are well documented, this research primarily comes from ship-based surveys and consequently individual level responses to discard availability are largely unknown. As part of a long-term study on lesser black-backed gulls (*Larus fuscus*) in the Netherlands, the fine-scale movements of adults were tracked with GPS tags throughout the breeding period. The aim of this study was to determine if lesser black-backed gulls were utilizing fishery discards in the Wadden Sea and to examine possible consequences of this behaviour. Within the Wadden Sea during weekdays, tracked birds predominately associated with zones where fishing vessels are known to operate (deep gullies). Across all individuals combined ($n = 40$), there was a significantly reduced use of the Wadden Sea during weekends when the fleets were not operating. Eight females, who markedly increased their use of the Wadden Sea during weekdays throughout the breeding period, were largely responsible for this pattern. The loss of discard resources on weekends primarily resulted in these eight individuals switching to terrestrial foraging areas. Nest attendance and total foraging time were consistent between weekdays and weekends, suggesting that resource shifts on weekends did not impact daily time budgets. As such, it appears that lesser black-backed gulls specializing on discard utilization are able to flexibly respond to the temporary loss of discards by switching to alternative resources.

Keywords: fishery discards, GPS tracking, individual specialization, *Larus fuscus*, lesser black-backed gull.

Introduction

Fisheries are known to impact various seabird species, directly and indirectly, and positively as well as adversely (Tasker *et al.*, 2000). For many species, discards are a valuable resource, being both easily accessible and relatively high in caloric value and are thus generally considered beneficial for seabird species (Furness *et al.*, 1988; Garthe *et al.*, 2006; Anderson *et al.*, 2011). Indeed, the increased availability of discards has been suggested to account for the growth of several seabird populations (Walter and Becker, 1997; Garthe *et al.*, 2006; Granadeiro *et al.*, 2013). For some species, however, this resource is a specious boon, as discards may only be ephemerally available until stocks are depleted or more insidiously, indirect negative effects, such as loss of natural foraging skills may prevail (Grémillet *et al.*, 2008). Faced with pressure to reform the amounts of discarded bycatch, the European Union (EU) has advocated a ban on discards (Borges, 2013). EU and coastal member states collectively manage fish stocks through the Common Fisheries Policy and while the details of the proposed reduction of discards are undecided at this time, when these revised policies go into effect, it may constitute a substantial change for marine ecosystems (Bicknell *et al.*, 2013). As such, it must be emphasized to consider the potential impacts on seabird populations, many of which may be dependent on this resource as a result of anthropogenic depletion of natural resources (Votier *et al.*, 2004).

Past tracking studies have revealed important factors related to seabird discard use such as sexual differences (Votier *et al.*, 2013), individual consistency (Granadeiro *et al.*, 2013), differences in foraging movement patterns (Bartumeus *et al.*, 2010), and the

relevance of scale (Bodey *et al.*, 2014). While several past studies have examined the response of specialist species to discard reductions, few studies have explored how a generalist species may respond to changes in the availability of fishery discards (but see Oro, 1996; Oro *et al.*, 1997). Furthermore, though recent work has focused on individual level responses, current knowledge of discard use by seabirds primarily comes from ship-based surveys (Camphuysen *et al.*, 1995). Extended tracking of GPS-tagged individuals offers the possibility to explore not only the extent of discard use, but also how individuals that rely on discards cope with the short-term absence of this resource.

The North Sea and the Wadden Sea are intensively used for commercial fishing. The predominant fisheries in the western Wadden Sea and in the Southern Bight (southern North Sea) are beam trawl fisheries for brown shrimp (*Crangon crangon*; mostly littoral fisheries) and, to a lesser extent, for flatfish (Pleuronectidae, mostly offshore fisheries). Such fishing methods historically produce the highest ratios of bycatch to target organisms (Van Beek *et al.*, 1990; Berghahn, 1994; Walter, 1997). In the eastern Wadden Sea, discards are suggested to constitute a substantial resource for many seabirds throughout the year (Walter and Becker, 1997).

The lesser black-backed gull (*Larus fuscus*) is a generalist feeder that forages primarily at sea, but in recent years increasingly on land, as well (Garthe *et al.*, 1999; Camphuysen *et al.*, 2006; Camphuysen, 2013). This species is known to capitalize on discards in the North Sea (Camphuysen, 1995). Indeed, the population breeding on the island of Texel has spectacularly grown in the last several decades; a trend that strongly mirrors increased efforts from the offshore Dutch beam trawl fleet (Spaans, 1998; Camphuysen, 2013). Prior studies have indicated that attendance of lesser black-backed gulls at offshore fishing operations is much higher than at inshore fishing vessels, which is consistent with the marine nature of this gull (Camphuysen, 1995; Walter and Becker, 1997). A previous GPS tracking study of this population, however, demonstrated that several individuals routinely visited the Wadden Sea (Camphuysen, 2013), an area most well known for its intertidal foraging opportunities (Van de Kam *et al.*, 1999). Yet, dietary analysis of this population suggested that individuals were not typically exploiting intertidal resources, but rather that their diet included a large proportion of demersal fish, which would only be available as discards (Camphuysen, 2013). This initial finding suggested that lesser black-backed gulls might in fact be foraging in association with shrimper fleets within the Wadden Sea.

The first aim of the current study was to examine if indeed this population of lesser black-backed gulls foraged for discards in the Wadden Sea. To explore this possibility, we first compared the temporal and spatial foraging patterns within the Wadden Sea at the population level to the spatial and temporal patterns of fishing vessels in the area. If lesser black-backed gulls forage in association with fisheries, we expected that the population-level use of the Wadden Sea would match the distribution of fisheries in both time and space. The second aim of our study was then to determine whether or not the utilization of fishery discards in the Wadden Sea was a specialized foraging strategy by examining sexual and individual differences in foraging patterns. Finally, if individuals specialized on fishery discard usage in the Wadden sea, we wanted to determine how aspects of individual time budgets, such as nest attendance, total foraging time, and habitat use, changed in the absence of fishery activities near the colony.

Methods

Study area

This study focuses on lesser black-backed gulls breeding in a colony on the island of Texel (The Netherlands, 53.00°N, 04.72°E), situated at the crossroads of the western Wadden Sea and the southern North Sea (Figure 1a). Strong tidal currents flow through a narrow passage (the Marsdiep) between the mainland (Den Helder) and the island Texel. The main foraging areas for this population include open sea (where birds forage on fish, including fisheries discards, swimming crabs, and Nereid worms), freshwater ponds, tourist resorts, agricultural land, sewage plants, rubbish tips, and mainland cities (where birds forage on mainly insects, mammalian prey, and domestic refuse). As of 2012, ~11 500 pairs of lesser black-backed gulls were breeding within the study area (Camphuysen, 2013).

Fisheries in the Wadden Sea are predominantly active during weekdays and return to the harbour for the weekend. Shrimpers, the major fishery, are active day and night during the week, and continue towing (and, hence, moving) while sorting the previous catch. Shrimpers are largely restricted to the deeper gullies of the Wadden Sea, but can still work in small creeks and inlets between mudflats when tidal conditions permit.

Data collection

GPS tracking

Adult breeding lesser black-backed gulls were trapped with walk-in traps halfway through incubation. Sexes were distinguished by biometrics (head plus bill length) with a 5% expected misidentification (Coulson *et al.*, 1983). Bill depth from base (mm), tarsus (mm), wing length (mm), and body mass (g) were also measured. Individuals were then colour-ringed and equipped with an 18 g solar-powered UvA-BiTS GPS logger (Bouten *et al.*, 2013), which was attached to the back of the bird with a Teflon ribbon three-strap backpack harness with one strap fitting across each wing and one strap below the crop (Shamoun-Baranes *et al.*, 2011). For each individual, the device and harness weighed $<4\%$ of the individual's body mass. A total of 46 breeding adult gulls were tagged between 2008 and 2012. The tracking system allowed for flexible measurement frequency while the device was deployed. In general, location fixes were obtained every 5–20 min across the breeding season. To minimize potential impacts on the birds from GPS attachment, we followed the recommendations made by Casper (2009). After tagging, all birds appeared to behave normally and promptly returned to their nests.

Breeding data

The breeding status of tagged individuals was monitored throughout the reproductive cycle. Nests were marked during egg laying and visited every third day from laying to fledging. Breeding phases were defined as (i) incubation, (ii) hatching, (iii) chick care (first 40 d after hatching), (iv) fledging (more than 40 d after hatching), and (v) failed breeding, which was assigned as the date when an individual lost its entire clutch or brood before fledging. Breeding phase was interpolated (nearest neighbour interpolation) between nest visits to assign a specific breeding phase to each GPS location.

Fishing vessel data

GPS locations of all commercial fishing vessels in the Wadden Sea region from 2008 to 2012 were used in the current study. As of 2005, Dutch commercial fishing vessels larger than 15 m are

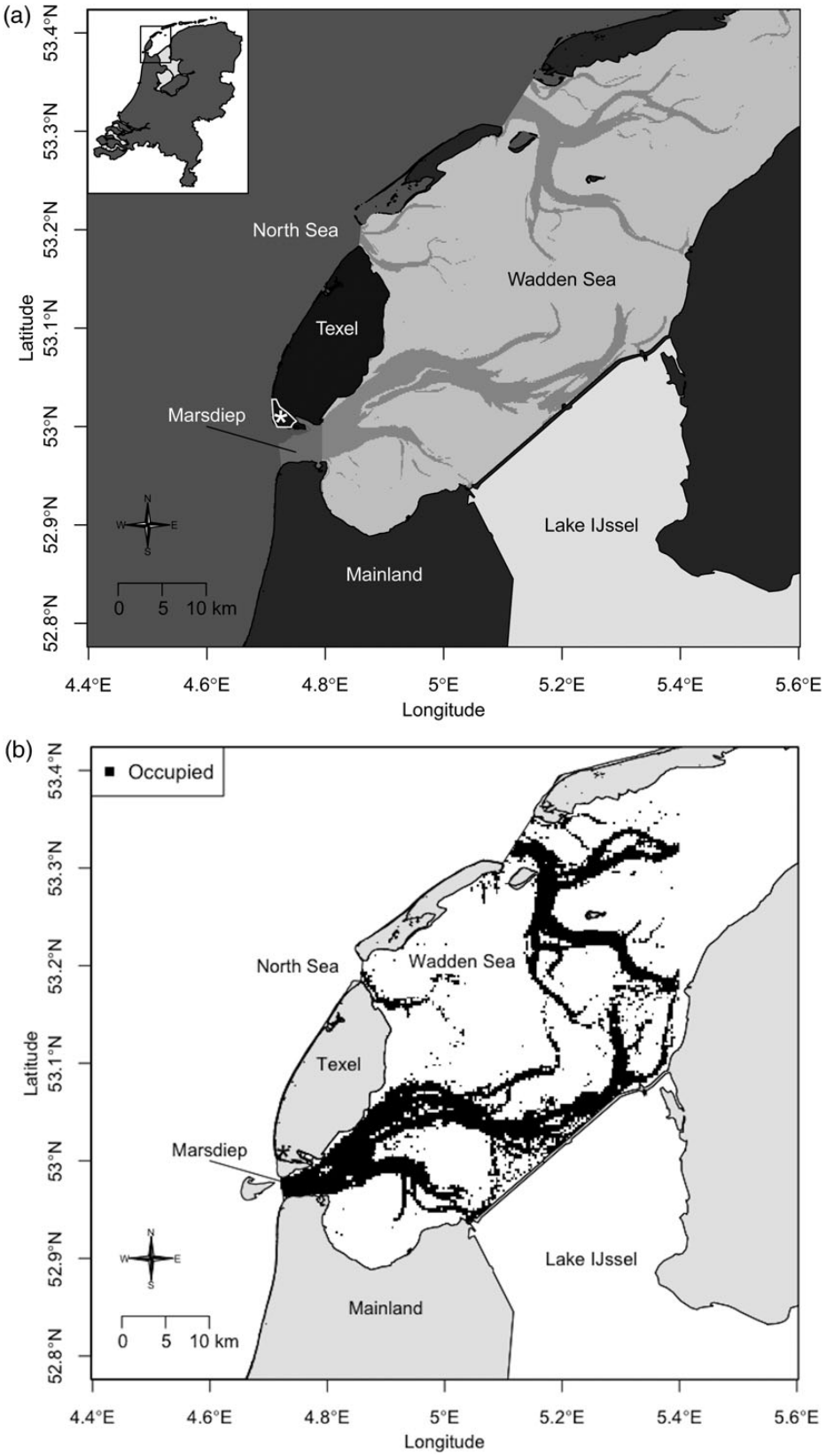

Figure 1. (a) Lesser black-backed gull colony on the island Texel, located between the Wadden Sea and the North Sea. The colony centre (white asterisk) is located at ~53.00°N, 4.72°E. The colony (white polygon) indicates the boundary used to define short trips and long (foraging) trips. Darker grey regions within the Wadden Sea are more than −1 m below sea level. The Marsdiep is a deep tidal race between the mainland and Texel. (b) Fishing vessel distribution within the Wadden Sea during weekdays in May–July from 2008 to 2012. Fishing vessel occupancy (at least one GPS location per cell) is presented in 200 m × 200 m grid cells. Colony location is shown as a black asterisk. The boundary between the Wadden Sea and the North Sea used in this study is marked by straight, thin lines connecting Texel to mainland and interconnecting the other islands.

equipped with a GPS transponder (VMS, vessel monitoring system) and transmit information on their ID, exact position, speed, and heading at a minimum of every 2 h. The VMS data are collected by the Netherlands Food and Consumer Product Safety Authority and made available in its raw format for research purposes. VMS data in itself do not provide information on gear type usage and species targeted by the fishery. Logbook data, however, where details on the fishing vessel itself, gear usage, and species caught are registered, do suffice for this need. In this study, VMS and logbook data were linked, to allow for analyses of gear-specific fisheries distribution at high spatio-temporal resolution, according to the methods described in Hintzen *et al.* (2012). In this study, only beam trawling vessels present in the VMS logbook dataset were analysed. To assess the temporal pattern of commercial fishing activity in the Wadden Sea, fishery activity (i.e. presence of a GPS location) was summarized per day of the week. We then used the temporal pattern in fishery activity for further comparative analysis with gull foraging activity.

Data processing

Statistical and spatial analyses were conducted in R, version 2.15.2 (R Core Team, 2012). ArcGIS was used for visualization of geographic data (ESRI, 2011).

Foraging trip classification

Using the known nest coordinates for each individual, distinct trips were identified. The nest location was buffered by a 150 m radius, which was taken to represent the nest zone. A trip was then defined as the last location fix before an individual left the nest zone until the next fix within the nest zone. Trips were classified as either short or long, depending on the zone utilized during the trip. Individuals are known to use the area directly surrounding the colony (see Figure 1a) for preening, bathing, and socializing, but rarely for foraging, as this area has minimal resources (Camphuysen, 2013). Trips that only occurred within this zone were labelled short trips, while trips that occurred at least partly outside of this zone were labelled long trips and were considered as periods of active foraging bouts. In this study, only long trips (hereafter, foraging trips) were considered.

Using data on the current breeding phase of each individual, it was possible to determine the breeding phase for each foraging trip. To avoid potentially confounding effects of altered foraging habits between breeding or non-breeding phases, only trips from breeding individuals were considered in the analysis. This period was defined as the first day of incubation until the end of the fledging period or alternatively until an individual lost the entire clutch or all young and became a failed breeder. Only trips wholly within the breeding period were included for analysis.

Data filtering

Occasional technical problems, such as low battery levels, resulted in irregular data coverage. An increased interval between observations increases the uncertainty of foraging locations and may result in merging multiple foraging trips. To avoid such problems, any trip with an interval >60 min between fixes was excluded from the analysis. Though 46 individuals were tagged and tracked, 40 individuals (24 females and 16 males) were tracked for more than 7 d (Supplementary Table S1). As we were interested in comparing the spatio-temporal use of the Wadden Sea to fisheries activity with potential weekly cycles, only individuals tracked for at least one full weekday and weekend period were analysed. Where individuals were tracked in multiple years, only the first year was considered.

Habitat data

Foraging use of five "habitat" zones (the Wadden Sea, the Marsdiep tidal-race, the North Sea, the island Texel, and the mainland) surrounding the colony was analysed (Figure 1a). Both the mainland and Texel were considered terrestrial habitats. Within the Wadden Sea, the Marsdiep tidal-race was separated, as this area is ecologically distinct from the Wadden Sea proper. Additionally, this area has constant ferry traffic.

Population level Wadden Sea use

Analysis of the fishery activity in the Wadden Sea revealed a clear weekly pattern (see Figure 2, results), which we used to distinguish between weekdays (Monday–Thursday) and weekends (Friday–Sunday). Using these two periods, we compared the temporal overlap in fishery activity with the foraging activity of the population in the Wadden Sea.

The total amount of foraging time spent within the Wadden Sea by the population of tracked individuals was determined by aggregating the amount of time spent across all foraging trips in the Wadden Sea during either weekdays or weekends. This was calculated by totalling the duration of all relocations within the Wadden Sea. The duration of relocations was determined by averaging the backward and forward intervals between relocations, yielding a "centred duration". Relocations were then assigned to each habitat type and the time spent within each habitat was summed. To analyse whether the proportion of foraging time in the Wadden Sea was different between sexes and between weekdays and weekends, hierarchical generalized mixed effect models (GLMMs) were formulated, using the foraging trip as the basic unit of analysis. Foraging trips were nested within individuals, which was assigned as a random factor; sex and weekend/weekday were considered as fixed factors. To find the most appropriate model, a multi-model comparison approach was applied (Burnham

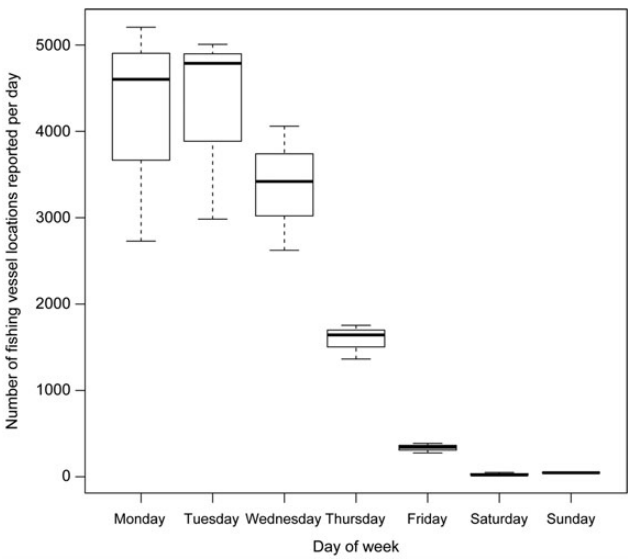

Figure 2. Count of reported fishing vessel locations per day within the Wadden Sea during May–July from 2008 to 2012. For each day of the week, a summary of data is provided as follows: the median (thick line), quartiles (outer box), and range (whiskers).

and Anderson, 2002), using the corrected Akaike information criteria (AICc). A set of five GLMMs was formulated and fitted with the response following a binomial distribution and a logit-link function. Specifically, the models with the following predictors were compared: (i) only individual effects (null-model) and no fixed effects, (ii) individual effects and sex as a fixed effect, (iii) individual effects and weekday/weekend as a fixed effect, (iv) individual effects and sex and weekday/weekend as fixed effects, and (v) model four with an additional interaction term between sex and weekday/weekend. GLMMs were fit and compared using the "lme4" and "AICcmodavg" packages in R (Bates *et al.*, 2014; Mazerolle, 2014).

Differences between weekdays and weekends were further explored spatially by mapping the time spent per cell within the Wadden Sea on weekdays and weekends using the "trip" package in R (Sumner, 2010). Additionally, to confirm that foraging areas within the Wadden Sea spatially coincided with commercial fisheries, a habitat selection analysis was conducted (Manly *et al.*, 2002). This analysis aims to determine whether individuals select particular habitat zones by controlling for habitat availability. Here, weekday habitat use was examined relative to zones occupied or unoccupied by commercial fishing vessels. To make this distinction, a raster (200 m resolution) based on the bathymetric data was used as a reference grid and cells where a fishing vessel had been present on weekdays from May to July during 2008–2012 were classified as occupied.

Fishery zones in the Wadden Sea were considered available if they overlapped with the home range estimated from all tracked individuals. Thus, this habitat selection method followed a design II approach where individuals are identified and tracked separately, but habitat availability is described at the population level (Thomas and Taylor, 1990). The home range in this study was defined as all used cells on a predefined 200 m × 200 m grid surrounding the colony (Soanes *et al.*, 2013). This method avoids several problems associated with estimating appropriate smoothing-parameters with autocorrelated data (Blundell *et al.*, 2001) and is well suited for datasets with a large number of relocations. Fishery use was then calculated per individual by summing the duration for occupied and unoccupied cells.

Habitat selection ratios for each individual were calculated as the quotient of used habitat and of available habitat. A global (population) habitat selection ratio based on individual averages was then calculated. Bonferroni 95% confidence intervals of global selection ratios were estimated from individual ratios. These intervals are used to define group selection or avoidance. An interval with an upper bound <1 indicates avoidance and conversely an interval with a lower bound >1 indicates selection. An interval including 1 indicates neither selection nor avoidance. Selection ratios were tested for significance using the log-likelihood χ^2 statistic. Habitat selection analyses were performed using the "adehabitatHS" package in R (Calenge, 2006).

Discard specialization

Having assessed population-level patterns of discard use, individual differences in Wadden Sea usage were then explored. We first determined whether or not there were individuals that made disproportionately higher use of the Wadden Sea during weekdays, but not during weekends. This subset of "discard specialists" was defined as individuals that showed a significantly higher use of the Wadden Sea during weekdays than during weekends (two-sided test for difference between two proportions, with a significance level of 0.05) and spent at least 10% of weekday foraging time in the Wadden Sea. This second criterion ensured that individuals chosen as discard specialists used the Wadden Sea as a significant foraging habitat. To evaluate whether discard use was observed across the breeding season, weekday to weekend differences in Wadden Sea foraging were separately evaluated during the incubating/hatching and chick-rearing/fledging breeding phases.

To examine whether these discard specialists were indeed selecting the Wadden Sea irrespective of its proximity to the colony, a habitat selection analysis was conducted, similar to the analysis employed to explore fishery associations. Here, however, availability was defined based on the home range of the identified discard specialists, rather than the whole population, as these were the individuals of interest. The relative availability of four habitat zones (the North Sea, Texel, the Wadden Sea, and the mainland) was determined by calculating the proportion of each of these habitats within the estimated home range. Habitat use by these individuals was then calculated as described above for each of these four habitat zones.

Possible implications for discard specialists were examined by comparing weekday with weekend habitat selection and shifts in time-budgets, specifically the proportion of foraging time, colony use, and nest attendance. Habitat selection shifts were evaluated by comparing the habitats that were selected on weekdays and weekends. Weekday and weekend foraging time and colony use was calculated relative to the total weekday and weekend hours tracked (excluding lost coverage), respectively. Nest attendance between weekdays and weekends was also explored. As lesser black-backed gulls are known to decrease nest attendance from the incubating/hatching to chick-rearing/fledging phase, changes in nest attendance were analysed separately between these periods (Camphuysen, 2013). Incubating/hatching and chick-rearing/fledging nest attendance proportions during weekdays and weekends were calculated relative to the total hours available during each period. The alternative hypotheses that average time-budget proportions differed between weekdays and weekends were tested using two-sided tests for equality of proportions, using a significance level of 0.05.

Results

Fishing vessel activity

Fishing vessels showed a clear weekly pattern in their activity during May–July from 2008 to 2012, with most of the activity occurring on Monday, Tuesday, and Wednesday, declining on Thursday and was almost completely absent on Friday through Sunday (Figure 2). The total number of fishing vessels increased from 2008 to 2012, with around 90 vessels operating in 2012.

Furthermore, fishing vessel activity displayed a clear spatial pattern, with vessels restricted to the deep gullies (see Figure 1a) in the Wadden Sea (Figure 1b). The presence of fishery vessels was then used to define fishery availability in the Wadden Sea.

Population level Wadden Sea use

After removing incomplete trips, there was an average (standard deviation, s) of 59 ($s = 46$) foraging trips per individual during the breeding period (total foraging trips, $n = 2352$). When aggregating all individuals, the average proportion of foraging hours spent in the Wadden Sea was 0.08 ($s = 0.11$) on weekdays compared with 0.01 ($s = 0.03$) on weekends (shown spatially in Figure 3a and b, respectively). The analysis of the alternative GLMMs explaining the proportion of time spent in the Wadden Sea (pT) identified the model including an effect by sex (males using Wadden Sea less),

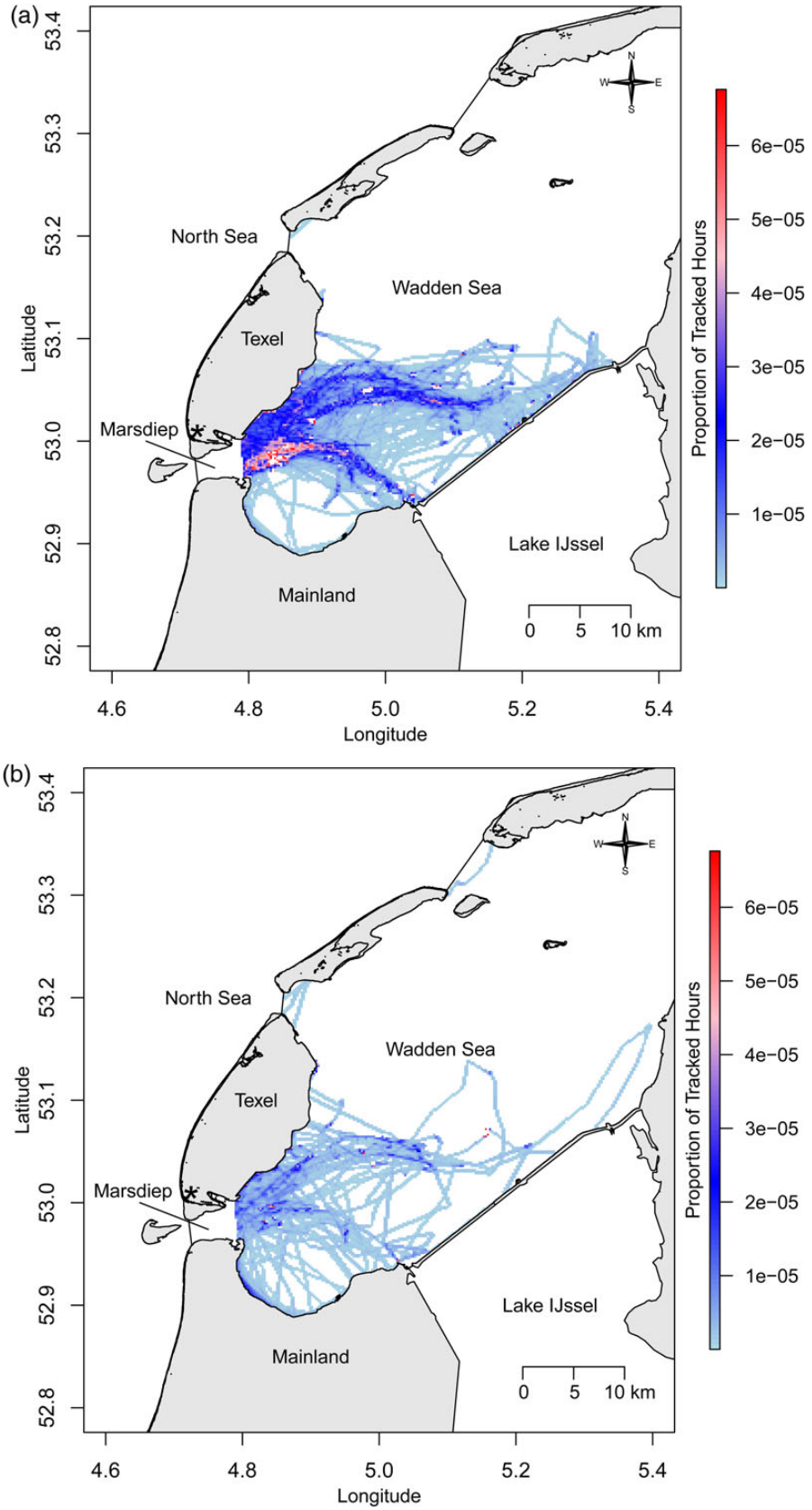

Figure 3. Relative foraging time for all individuals together during (a) weekdays and (b) weekends in the Wadden Sea. Units are the proportional number of hours relative to total weekday (a) and weekend (b) foraging hours per 200 m cell, respectively. The western cut-off is the Wadden Sea – Marsdiep tidal-race boundary. Colony location is shown as a black asterisk.

weekday/weekend (less usage during weekend) as well as an interaction between sex and weekday/weekend (a stronger weekend effect for females) as the most suitable model by far: $\text{logit}(\text{pT}) = -5.5 - 2.3 \times M - 7.5 \times W + 2.2 \times MW$ (with M, the effect of being male; W, the effect of weekend; and MW, the interaction effect of weekend and being male). All parameters in this model were highly significant (all $p < 0.001$) with an overall model significance of ($\chi^2 = 2 \times 10^6$, $p < 0.001$) and an explained deviance of 0.22 (Supplementary Table S2).

Within the Wadden Sea during weekdays, lesser black-backed gulls used zones of commercial fishery activity disproportionately more than was available ($\chi^2 = 33.44$, $p = 0.001$). Thus, during weekdays, the areas occupied by commercial fishing vessels were clearly selected, while unoccupied areas were avoided (Table 1).

Discard specialization

Individuals varied greatly in their use of the Wadden Sea. Only 25 of the 40 individuals analysed foraged at some point within in the Wadden Sea during the tracking period. These individuals made an average of 10 ($s = 16$, $n = 396$) foraging trips that occurred at least partly within the Wadden Sea, with an average of 9.0 ($s = 14$, $n = 350$) foraging trips during weekdays, but only 1.2 ($s = 1.9$, $n = 48$) foraging trips during weekends (Supplementary Table S1). However, of all tracked individuals, only eight showed statistically significant differences between weekday and weekend use in the Wadden Sea and spent at least 10% of their time there. All eight individuals were female.

On average, these eight discard specialists spent 0.24 ($s = 0.11$) of weekday foraging hours and 0.04 ($s = 0.02$) of weekend foraging hours within the Wadden Sea, which was significantly different ($p < 0.001$). This trend was consistent across the breeding season. During the incubation and hatching phases, the average proportion of foraging hours spent by the discard specialists in the Wadden Sea was significantly different, 0.27 ($s = 0.14$) of foraging hours during weekdays and 0.01 ($s = 0.01$) of foraging hours during weekends, $p < 0.001$. Similarly, during the late breeding phases (chick-rearing and fledging), the average proportion of foraging time in the Wadden Sea between weekdays, 0.27 ($s = 0.13$), and weekends, 0.04 ($s = 0.03$), was significantly different, $p < 0.001$.

Overall, during weekdays, the discard specialists did not use habitat in proportion to availability ($\chi^2 = 9.50$, $p = 0.023$), indicating that the group was selecting or avoiding certain habitats (Table 2). During weekdays, the Wadden Sea was the only selected habitat by the discard specialists. This group showed no selection that was disproportionate to availability for Texel and the mainland, but actively avoided the North Sea. There was substantial individual variation, however, in the selection ratios for Texel. Overall, during weekends, the proportion of habitat used by the discard specialists was not significantly different from the proportion of available habitat used ($\chi^2 = 4.85$, $p = 0.182$), indicating neither selection nor avoidance for all habitats.

Scavengers foraged for 0.62 ($s = 0.13$) of weekday hours and for 0.50 ($s = 0.13$) of weekend hours, which suggests that there was no significant difference in total foraging time between these two periods ($p = 0.311$). Similarly, the proportion of hours spent within the colony during weekdays and weekends (0.02 ± 0.02 and 0.02 ± 0.03, respectively) was not significantly different ($p = 0.279$).

For the discard specialists as a group, average nest attendance between weekdays and weekends during the incubation/hatching phase was also not significantly different (0.52 ± 0.11 of weekday hours to 0.53 ± 0.08 of weekend hours, $p = 0.472$). Similarly, there were no differences in average nest attendance between weekdays and weekends during the chick care/fledging phases (0.29 ± 0.16 of weekday hours to 0.30 ± 0.20 of weekend hours, $p = 0.342$).

Discussion

GPS locations reported by fishing vessels within the Wadden showed a strong weekly rhythm, with markedly decreased activity during Friday–Sunday. This periodization of fishery activity offered a prime context to explore whether use of the Wadden Sea was driven by the availability of discards. Thus, to more closely examine the extent and nature of this behaviour, foraging activities in the area were compared between periods with and without commercial fishing activity.

Lesser black-backed gulls breeding on the island of Texel can forage in a range of habitats and on a variety of resources. Preliminary analysis of GPS tracking data from adults breeding on Texel revealed that individuals periodically foraged within the Wadden Sea. Yet past dietary analysis from this colony (Camphuysen, 2013) did not include intertidal prey, but rather frequently included benthic fish, which would only be available as discards. As such, it seemed that individuals foraging in this area were likely scavenging for discards from fishing vessels.

Our study showed that, at the population level, foraging time in the Wadden Sea per trip was significantly reduced during weekends. Average weekday use across all tagged individuals during their breeding period was relatively low (5.8%), but weekend foraging within the Wadden Sea was virtually absent (0.8%). As such, as a population, lesser black-backed gulls did use the Wadden Sea, though in small measure and only when commercial fisheries were active.

Table 1. Habitat selection of zones occupied or unoccupied by fishing vessels.

Fishing vessels	Available	Used	Wi	s.e.	CI lower	CI upper	Index
Unoccupied	0.57	0.31	0.55	0.04	0.46	0.64	−
Occupied	0.43	0.69	1.59	0.05	1.48	1.70	+

Available refers to the habitat available to the population (areas occupied or unoccupied by fishing vessels), while used is the average habitat use of the population. Wi is the selection index. The standard error (s.e.) and the associated confidence intervals (CIs) are also provided. The index refers to selection: −, avoided; +, selected.

Table 2. Habitat selection by discard specialists ($n = 8$).

Habitat	Available	Used	Wi	s.e.	CI lower	CI upper	Index
Weekday							
Mainland	0.23	0.15	0.63	0.18	0.19	1.07	o
North Sea	0.72	0.43	0.61	0.09	0.39	0.82	−
Texel	0.02	0.11	6.15	2.20	0.66	11.64	o
Wadden Sea	0.03	0.31	8.87	1.55	4.99	12.74	+
Weekend							
Mainland	0.23	0.24	1.04	0.34	0.20	1.88	o
North Sea	0.72	0.54	0.75	0.10	0.51	1.00	o
Texel	0.02	0.19	10.58	3.87	0.91	20.26	o
Wadden Sea	0.03	0.03	0.85	0.28	0.16	1.55	o

Wi is the selection index. The standard error (s.e.) and the associated confidence intervals (CIs) are also provided. The index refers to selection: o, neutral; −, avoided; +, selected.

Furthermore, there was a clear selection for zones of fishery activity during weekdays. Thus, lesser black-backed gull foraging and commercial fishing within the Wadden Sea followed the same spatial and temporal pattern. Aside from actually foraging for discards, however, an alternative explanation for this observed pattern might be that birds are initially attracted to areas of higher activity, but do not partake in discard foraging themselves. Some gull species are known to locate prey patches based on the presence of a flock (Götmark *et al.*, 1986) and in this way, lesser black-backed gulls might be drawn to the Wadden Sea during periods of discard scavenging, and yet not forage for discards. The combination of spatial and temporal overlap between foraging movements and commercial fishing activity, as well as the frequent occurrence of benthic fish in this population's diet (Camphuysen, 2013), which could only come from discards, however, strongly suggests that tracked gulls do in fact forage for discards in this area.

Discard foraging in the Wadden Sea was highly sex-specific with females showing an increased use of this habitat during weekdays and males showing low use of this habitat at all times. This supports earlier observations by Camphuysen (2013) that individuals using the Wadden Sea from this population are predominately female. Past studies have similarly shown sex-specific discard use, such as in northern gannets (*Morus bassanus*), where males are known to utilize this resource more than females (Stauss *et al.*, 2012; Votier *et al.*, 2013). The overall effect of sex on discard foraging, however, requires further examination as other sources of discards, such as from North Sea fisheries, were not explored in this study.

Discard scavenging is a competitive activity that potentially favours larger and more powerful individuals. Camphuysen (2013) suggested that this might explain the higher attendance of male lesser black-backed gulls to offshore beam trawlers in the North Sea. It was further remarked that female lesser black-backed gulls foraging within the Wadden Sea would likely face strong competition from the larger and more powerful herring gulls (*Larus argentatus*; Camphuysen, 1995). As such, competition at shrimp trawlers within the Wadden Sea might actually be higher than when foraging with conspecifics in the North Sea. Such niche segregation between male and female lesser black-backed gulls might represent risk partitioning or alternatively, it may suggest that larger size does not necessarily yield a competitive advantage, but that other physical factors are more relevant. At this time, however, the mechanisms behind this pattern are an open question.

Taken together, these findings demonstrate that lesser black-backed gulls use the Wadden Sea almost exclusively to scavenge for discards and that this habitat is not utilized in the absence of fishing fleets. Still, given this habitat's proximity to the colony (within 10 km), it would seem to be an energetically efficient foraging area. A likely explanation for the nearly complete abandonment of the Wadden Sea during weekends is likely a lack of natural prey (Lotze *et al.*, 2005).

Discard specialists

For the group of eight discard specialists (all female), separate habitat selection analyses during weekdays and weekends showed strong shifts in habitat preference, from a preference for the Wadden Sea during weekdays to neutral habitat selection during weekends for all habitats. This test provides similar information to standard comparisons of proportions, but controls for availability, and thus provides a stronger test by indicating whether the observed patterns are the result of actual selection rather than simply the product of differences in availability.

Several studies have attempted to address the question of whether individual seabirds specialize in discard scavenging (Votier *et al.*, 2010; Ceia *et al.*, 2012; Granadeiro *et al.*, 2013). Findings thus far, however, have been mixed or were based on relatively few foraging trips. By tracking individuals across the entire breeding season, this study covers a uniquely long temporal scale and thus provides evidence of individual specialization on discards in lesser black-backed gulls.

By identifying clear discard specialists, it was possible to explore potential impacts of this lifestyle choice as individuals foraging on discards in the Wadden Sea during weekdays were forced to switch foraging strategies during weekends. This situation offers a microcosm to assess how a fisheries landing obligation under EU legislation might affect marine-scavenging seabirds. The responses of discard specialists identified in this study were highly variable between individuals. The fact that most individuals showed mixed preferences for their second most selected habitat might account for this irregular habitat shift on weekends. If forced to switch from a preferred habitat, it is plausible to expect that individuals would respond by increasing attendance at their second most familiar habitat (Weimerskirch, 2007). Still, on weekends, there was a general shift towards terrestrial habitats for the eight female discard specialists. That these individuals increased time in terrestrial areas as opposed to the North Sea was somewhat surprising considering the marine nature of this species. One explanation for the switch towards terrestrial foraging habitats might be sex-specific niche segregation. With male lesser-black backed gulls predominately foraging offshore in the North Sea, sexual segregation may reduce the risk of intraspecific competition, a strategy that has been demonstrated in several seabird taxa (Ishikawa and Watanuki, 2002; Quintana *et al.*, 2011; Stauss *et al.*, 2012). Consequently, females may be deliberately limiting spatial overlap with male conspecifics by foraging on the mainland.

Food availability is the predominant constraint on seabird breeding success (Cairns, 1992) and as such, the ability of individuals to switch resources is of critical importance when discards decline. Indeed, gulls and skuas are generally expected to respond by switching to alternative prey or by resorting to kleptoparasitism (Oro *et al.*, 1997; Camphuysen and Gronert, 2010; Bicknell *et al.*, 2013). In this study, while the responses of discard specialists were variable, these individuals tended to switch towards terrestrial habitats on weekends. The same trend, however, was also observed for non-scavenging females (data not shown). This general shift towards terrestrial foraging, e.g. farmland or city refuse, on weekends requires further attention.

Despite a clear resource shift on weekends, individual time budgets did not appear to be negatively impacted for the group of discard specialists. Between weekdays and weekends, nest attendance was not significantly different and similarly, the proportion of total foraging time and "colony-use" was consistent during these periods. We interpret this as an indication that discard specialists are sufficiently capable of adapting foraging behaviour in the temporary absence of their preferred resource. Still, an alternative explanation is that foraging time is constrained by nest attendance and so measures of foraging efficiency would be more informative.

Tracked birds from this study showed consistently increased weekday foraging within the Wadden Sea across the breeding period. Conversely, Schwemmer and Garthe (2005) found an association between fishing effort and lesser black-backed gull distributions in the Southeastern North Sea only in July and August. The authors offered two interpretations of this finding: reduced

constraints on foraging distances in the end of the breeding period and seasonal variation in the abundance of other prey options, such as swimming crabs (*Liocarcinus* spp.). The comparatively proximity of shrimp trawlers in the Wadden Sea to the colony on Texel might explain consistent discard scavenging throughout the breeding cycle. Differences in food availability between locations or years might account for these disparate findings as well.

Ultimately, it appears that lesser black-backed gulls feeding on discards in the Wadden Sea are able to flexibly respond to the temporary loss of this resource. While this might indicate a promising ability of other species to cope with the sudden loss of discards, the routine disappearance of discards on weekends may have afforded a unique opportunity for this population to develop a dual-specialization. Elsewhere, abrupt changes to discard quantities lasting several weeks and overlapping with the breeding season were shown to negatively affect egg size and breeding success in populations of lesser black-backed gulls and yellow-legged gulls (*Larus michahellis*; Oro *et al.*, 1995; Oro, 1996). As such, it is not necessarily the case that other lesser black-backed gull populations will respond as flexibly as the individuals in this study seem to have done. While there is a clear need to reduce discard production, this change must come at the level of reforming fishing practices more generally, as simply reducing discards without curtailing fishing rates will diminish resources for seabird populations without replacing alternatives (Heath *et al.*, 2014). The flexibility of discard specialists demonstrated in this study suggests that such changes should be gradually implemented, which might allow for individuals to develop alternative foraging skills over time.

Supplementary data

Supplementary material is available at the *ICESJMS* online version of the manuscript.

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