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Attracted to the outside: a meso-scale response pattern of lesser black-backed gulls at an offshore wind farm revealed by GPS telemetry

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Among seabirds, lesser black-backed gulls (*Larus fuscus*) are considered to be at high risk of colliding with offshore wind turbines. In this respect, we used GPS tracking data of lesser black-backed gulls caught and tagged in two colonies along the Belgian North Sea coast (Ostend and Zeebrugge) to study spatial patterns in the species' presence and behaviour in and around the Thornton Bank offshore wind farm (OWF). We found a significant decrease in the number of GPS fixes of flying birds from up to a distance of at least 2000 m towards the middle of the wind farm. Non-flying birds showed a similar avoidance of the wind farm interior, yet presence strongly peaked right at the wind farm's edge, demonstrated to represent gulls perching on the outer turbine jacket foundations. The findings of this study reveal a strong within-wind farm variability in bird density, a most crucial parameter in collision risk modelling. The method presented here is straightforward and similar studies conducted at other wind farm sites on a range of large gull species (*Larus* sp.) would allow to assess the potential and species-specific variation in meso-scale response patterns and to gain insight in the underlying ecological incentives, which in turn would provide widely applicable and much-needed input for (cumulative) collision impact assessments.

Keywords: avoidance, collision risk, GPS telemetry, impact assessment, lesser black-backed gull, offshore wind farm

Introduction

Parallel with the fast growth of the offshore wind industry, an increasing number of studies are assessing offshore wind farm (OWF) impacts on marine wildlife (e.g. Dierschke *et al.*, 2016; Cook *et al.*, 2018; Perrow, 2019). Seabirds in particular are of great concern because of multiple issues such as barrier effects, displacement from favoured feeding grounds and increased collision mortality, acting either daily in central place foragers or seasonally during migration (Drewitt and Langston, 2006; Fox *et al.*, 2006). But even when empirically demonstrated and quantified, translating such effects into population impact through changes in mortality and/or productivity rates has proven to be highly challenging (Searle *et al.*, 2014; O'Brien *et al.*, 2017).

Furness *et al.* (2013) ranked lesser black-backed gull (*Larus fuscus*) in the top three of seabird species most at risk of colliding with turbine blades, particularly due to the fact that these gulls frequently fly at rotor height (30% of the flights). This, combined with the lack of a consistent avoidance response towards OWFs (Dierschke *et al.*, 2016; Vanermen and Stienen, 2019) and its high abundance in the North Sea, makes the lesser black-backed gull a potential victim of significant impact at population level (Brabant *et al.*, 2015). Reliably assessing collision risk is, however, highly dependent on qualitative data of presence and avoidance rates. In fact, birds may avoid a wind farm area as a whole ("macro-avoidance") or only particular turbines or arrays ("meso-avoidance"), but may also perform last-second avoidance actions to prevent a collision with moving rotor blades ("micro-avoidance") (Cook *et al.*, 2018). Ship-based or aerial surveying is currently the most often applied strategy for studying seabird—wind farm interactions and allow for estimations of macro-avoidance rates. Yet major knowledge gaps persist on meso- and micro-scale avoidance, nocturnal bird behaviour and whether or not responses vary according to meteorological circumstances. Collision risk models further tend to assume a constant bird flux across the wind farm (Band, 2012), while this may not reflect reality. Addressing these aspects requires detailed knowledge on individual bird movements, which can be obtained from targeted telemetry studies (Masden and Cook, 2016; Cook *et al.*, 2018). Indeed, when analysing fine-scale movements of lesser black-backed gulls inside OWFs using GPS tracking, Thaxter *et al.* (2018) found evidence of meso-scale avoidance, as such informing the on-going discussions on avoidance rates and collision risk modelling (Green *et al.*, 2016; Skov *et al.*, 2018). The use of GPS data further allows to link potential collision mortality to the colony (or colonies) of origin which may help to inform local bird conservation issues.

The Belgian coast hosts internationally important breeding numbers of lesser black-backed gull, and the Flemish government has committed to preserve at least 1920 breeding pairs (Paelinckx *et al.*, 2009). Most of the current Belgian breeding population of about 3000 pairs breeds in Zeebrugge and Ostend. With the Thornton Bank OWF in the southern North Sea within foraging range, GPS tagging of lesser black-backed gulls at both colonies offered the opportunity to study fine-scaled spatial patterns in the gulls' presence and behaviour in and around this particular wind farm. Based on clear indications of attraction to the outer turbines observed in great black-backed gulls (*Larus marinus*) during ship-based monitoring surveys at the Thornton Bank OWF (Vanermen *et al.*, 2017), this study specifically aimed at investigating the effect of distance to the wind farm edge on the encounter rate of tagged lesser black-backed gulls, with special attention to the role of turbine-associated perching behaviour.

Material and methods

Data collection and processing

Between 2013 and 2017, 83 lesser black-backed gulls breeding in Zeebrugge (51.348°N 3.173°E, 77 birds) and Ostend (51.233°N 2.931°E, 6 birds) have been equipped with a UvA-BiTS tracker generating three-dimensional GPS fixes (Bouten *et al.*, 2013; Stienen *et al.*, 2016). During this period, these sites hosted 70–98% of the Belgian population of lesser black-backed gulls. The deployment of GPS trackers was authorized by the ethical committee for animal experiments (license number CDE2013–73) and conducted in accordance to Flemish and Belgian legislation. To fit the GPS trackers, all individuals were caught on their nests during incubation using walk-in traps or clap nets. Trackers were attached using a wing harness of Teflon ribbon threaded with a nylon string (Stienen *et al.*, 2016). The wing harness attachment method is considered to be the most appropriate for long-term deployments, and lesser black-backed gulls have not been demonstrated to suffer from tag effects in terms of breeding productivity or overwinter return rates (Thaxter *et al.*, 2014, 2016; Kavelaars *et al.*, 2018). The collected data were remotely transmitted to a base station located inside the colonies.

First we made a selection of offshore GPS fixes within a distance of 1–80 km from the colony. Tracking resolution varied strongly from 10 to 3600 s resulting from the different needs and priorities of the GPS data end-users. To obtain an unbiased dataset and avoid temporal correlation between records (Ross-Smith *et al.*, 2016; Shamoun-Baranes et al., 2017), tracks with a resolution lower than 20 min were omitted (0.9% of the data) and all remaining data were subsampled to a 20-min resolution, representing the original resolution for 52% of the total (offshore) tracking time. Because the Thornton Bank OWF was only fully operational from the summer of 2013 onward, GPS fixes collected in 2013 were discarded from the dataset.

Displaying the resulting subset of GPS records (59 493 fixes of 63 individuals) shows that the Thornton Bank OWF and its control area are located within the distribution range of lesser black-backed gulls originating from Ostend and Zeebrugge (Figure 1). In this data selection, 10 individuals generated data over all four study years (2014–2017), with a median of 2 years of data per individual. Considering their migratory behaviour, all GPS fixes included were collected in the period March–September, 85% of which in April–July.

Birds were considered flying when their recorded ground speed exceeded 4 m/s, a cut-off speed coinciding with the minimum between the two distinctive modes of the histogram in Figure 2. Speeds below 4 m/s are indeed expected to discern a variety of behaviours (such as standing, resting, walking, floating, soaring and tortuous flight) from active flight (Baert *et al.*, 2018).

Modelling exercises

A grid of 250 × 250 m cells up to a distance of 3000 m to the nearest turbine was used to gain a general insight in the effect of distance to the wind farm on the encounter rate of lesser black-backed gulls. Considering the presence of the Northwind OWF just north of the Thornton Bank and anticipating on possible combined effects of both wind farms, it was not feasible to extend this distance beyond 3000 m, and grid cells located within 3000 m from Northwind turbines were discarded accordingly (Figures 3 and 4). For each of the 1931 resulting grid cells, we determined the distance from their centroid to the Thornton Bank wind farm edge, assigning negative distances to grid cell centroids falling inside the wind farm boundaries. As such, distances ranged from −1267 m inside ($n = 362$) up to 2999 m outside ($n = 1569$) the wind farm. An overlay of this grid with the GPS fixes of bird individuals with at least 20 records inside the study area ($n = 23$, see Table 1) resulted in a total of 1928 fixes, 27% of which were categorized as "flying" and 73% as "non-flying." The number of fixes per grid cell and per individual (N_1), assessed both for "flying" and "non-flying" birds, was then modelled including distance to the wind farm edge (D_{owf}) as a thin-plate smoother (limiting the number of knots k to 6) and distance to the coast (D_{coast}) as a linear effect. In a next step, we included a factor representing the presence/absence of a turbine or platform inside the grid cells ($TB_{pres/abs}$) allowing to perform separate predictions for encounter rates either near or in between the constructions, thus giving the following formulas:

$$N_1 \sim D_{coast} + s(D_{owf}, k = 6)$$

$$N_1 \sim D_{coast} + s(D_{owf}, by = TB_{pres/abs}, k = 6)$$

Bird identity was included in the models as a random intercept. We fitted these mixed models applying Poisson, negative

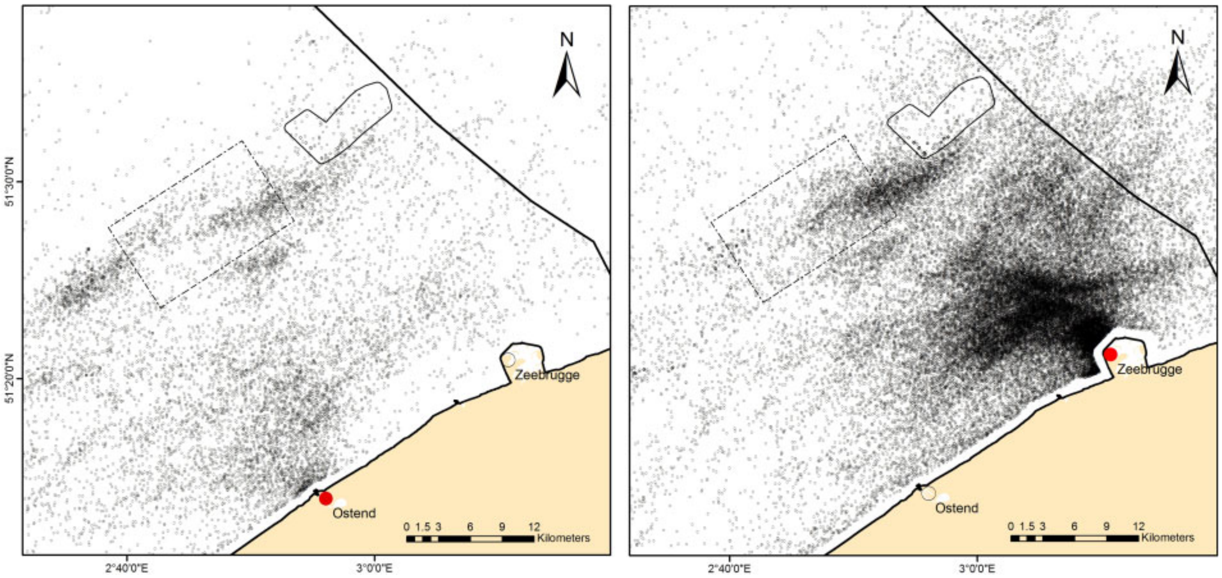

Figure 1. Twenty minute interval offshore GPS fixes (dots) of lesser black-backed gulls originating from Ostend (left panel, 6 individuals) and Zeebrugge (right panel, 57 individuals) (period 2014–2017); the figure further shows the Belgian North Sea border (thick line), the Thornton Bank OWF impact area (thin line), and the OWF control area (dashed line).

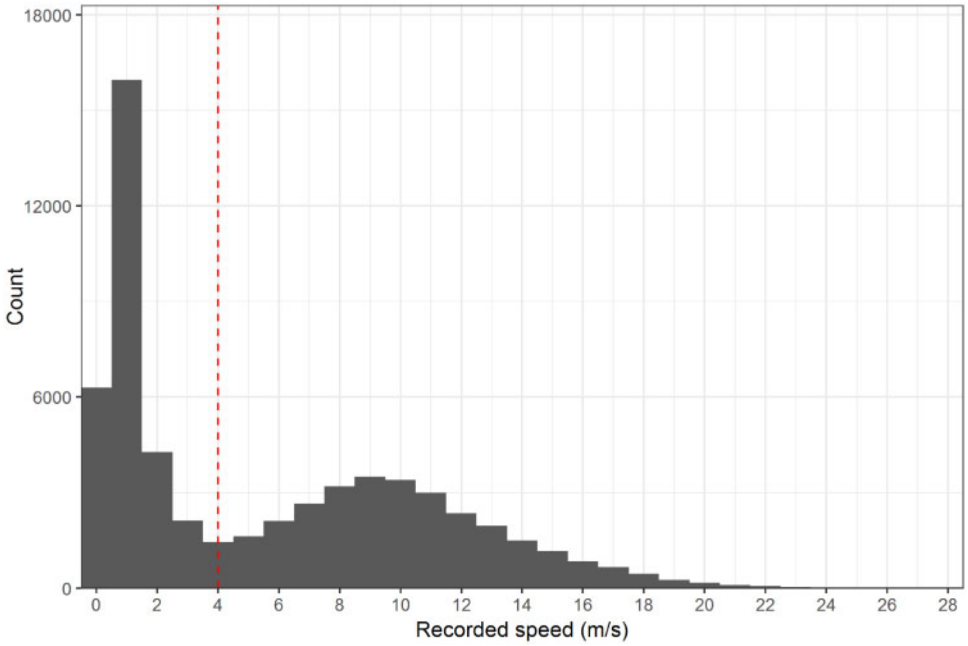

Figure 2. Recorded ground speeds in offshore tracks of lesser black-backed gulls; the cut-off speed of 4 m/s to distinguish between "flying" and a variety of "non-flying" behaviours is shown by the dashed line.

binomial and zero-inflated Poisson distributions, and continued with a negative binomial model for non-flying and a Poisson model for flying birds based on the corresponding Akaike information criterion (AIC) values (Akaike, 1974).

In a following step, we selected all GPS fixes within 100 m from the jacket founded turbines in order to study the gulls' presence on or near the turbine foundations. Note that the Thornton Bank wind farm includes 1 transformer platform and 54 turbines, 48 of which are installed on jacket and six on gravity-based foundations (Figure 3). The latter were not taken into account in this analysis because no fixes were recorded on or near the gravity-based foundations. Neither did we include the (single) transformer platform because of its highly different characteristics. As such, we tested whether the time spent on or near a jacket foundation differed between outer and inner turbines, which would indicate a meso-scale response pattern. The

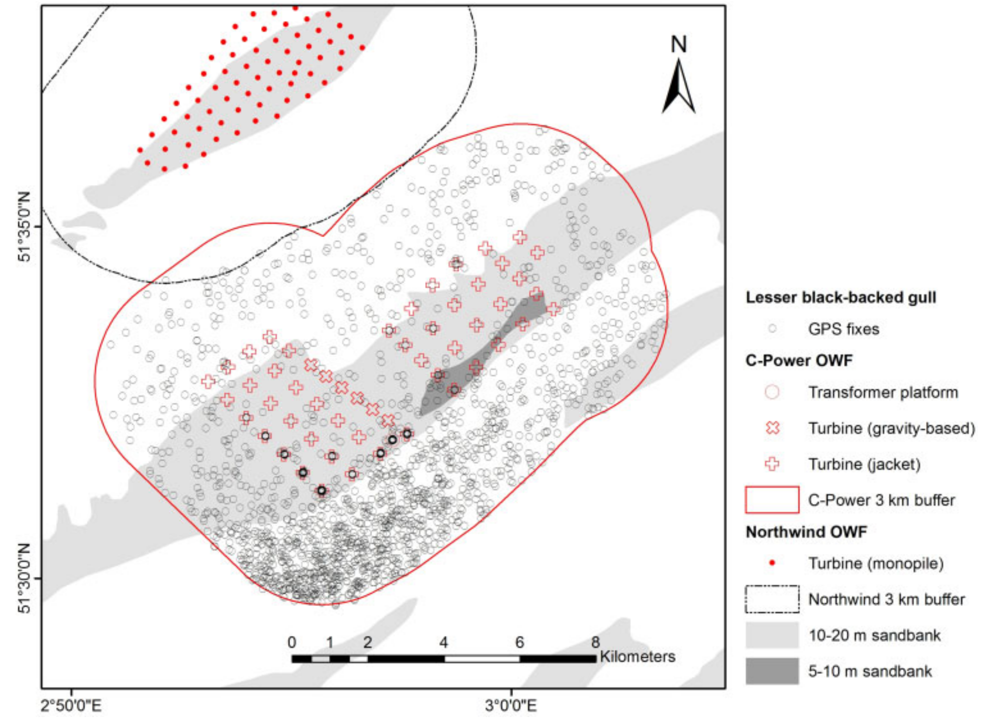

Figure 3. GPS fixes of lesser black-backed gulls within the 3 km buffer zone of the Thornton Bank wind farm (and outside the Northwind buffer zone) as used in the analysis of the effect of distance to the wind farm edge on the encounter rate of tracked gulls.

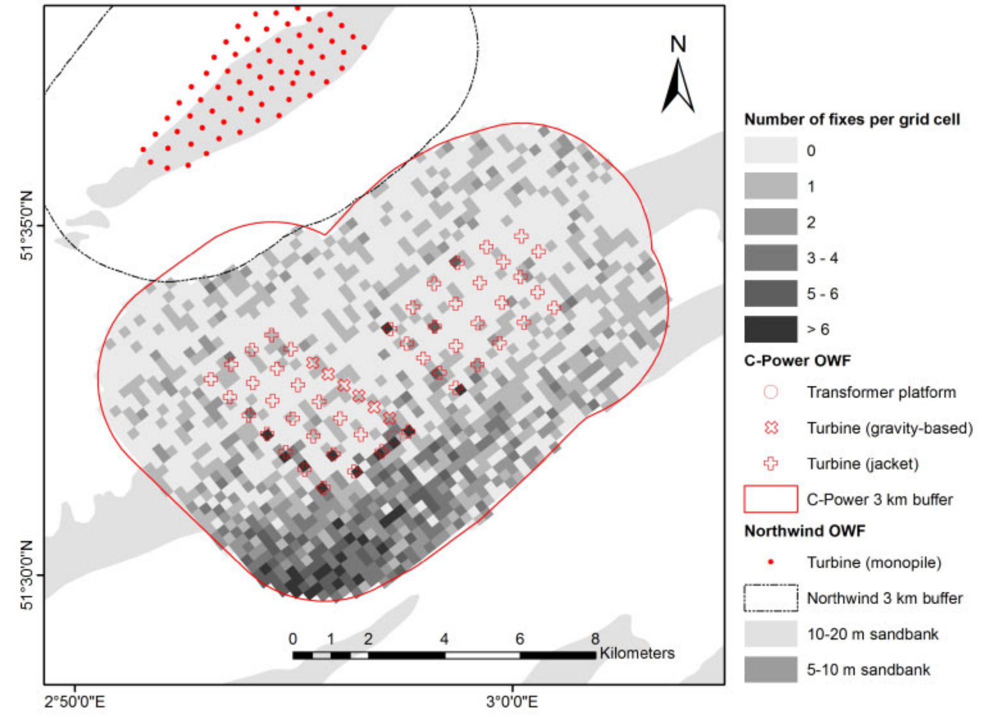

Figure 4. The number of GPS fixes of lesser black-backed gulls per 250 × 250 m grid cell (aggregated across individuals and flying/non-flying behaviour) as used in the analysis of the effect of distance to the wind farm edge on the encounter rate of tracked gulls.

Table 1. Number of tracked individuals per year and per colony included in the analysis of the effect of distance to the wind farm edge on the number of GPS fixes.

	2014	2015	2016	2017	Total
Ostend	0	0	4	4	**4**
Zeebrugge	10	14	15	12	**19**

number of GPS fixes per 100 m turbine buffer zone and per individual (N_2) was modelled using distance to the coast (D_{coast}) and an inner/outer turbine factor ($TB_{inner/outer}$) as explanatory variables:

$$N_2 \sim D_{coast} + TB_{inner/outer}$$

Again, bird identity was included in the model as a random intercept. Based on the AIC, a negative binomial distribution performed better compared with a Poisson distribution and its zero-inflated alternative.

All data processing and analyses were performed in R version 3.5.2 (R Core Team, 2018) using RStudio (RStudio Team, 2016) making use of the following packages (in alphabetical order): data.table (Dowle and Srinivasan, 2017), ggplot2 (Wickham, 2009), gridExtra (Auguie, 2017), MASS (Venables and Ripley, 2002), mgcv (Wood, 2017), plyr (Wickham, 2011), pscl (Zeileis *et al.*, 2008), rgdal (Bivand *et al.*, 2017), rgeos (Bivand and Rundel, 2017), spatialEco (Evans, 2017), and sp (Pebesma and Bivand, 2005).

Results

Distance to the wind farm edge

Both for flying and non-flying birds, the distance smoother appeared to be highly significant ($p < 0.001$, see Tables A1a and A2a in Appendix). For flying birds, the resulting model predicted a gradual decrease in the number of fixes from up to a distance of at least 2000 m towards the middle of the wind farm, and slightly increased presence along the wind farm edge. For non-flying birds too, the model predicted a minimum number of fixes inside the wind farm, yet with a much more distinct secondary peak in presence right at the wind farm's edge (Figure 5).

When further including a factor representing the presence/absence of a turbine or platform inside the grid cells, this did not lead to model improvement in case of flying birds, yet to a much lower and better AIC for non-flying birds ($\Delta AIC = 423.5$, Tables A1b and A2b in Appendix). Model predictions for grid cells without anthropogenic structures showed a steady increase in the estimated number of non-flying fixes up to a distance of nearly 2000 m from the OWF edge (with no more secondary peak in occurrence, see Figure 6, right panel), while grid cells including the turbines and transformer station were characterized by a stronger and almost exponential increase in non-flying fixes going from the middle of the wind farm up to its edge (Figure 6, left panel). All model results are summarized in Appendix (Tables A1 and A2).

Association with turbine foundations

Lesser black-backed gulls were regularly recorded on or near the anthropogenic structures of the Thornton Bank OWF ($n = 285$), with an apparent preference for the south-western corner of the wind farm (Figures 3, 4, and 7). Within the 100 m turbine buffer zones, 95% of the GPS fixes refer to non-flying birds. In the OWF as a whole the percentage of non-flying birds amounted to 86%, which in turn is higher than the percentages found for the OWF control area (77%) and the offshore data in general (60%) (see Figure 1 for the data selection polygons).

Out of the 31 individuals entering the wind farm boundaries, 16 different birds were recorded at least once near or on the jacket founded turbines and the transformer platform. Based on the proportion of fixes within the 100 m turbine buffer areas to the total number of fixes within the OWF boundaries ($n = 510$), the tagged lesser black-backed gulls spent 56% of their time in the direct vicinity of the jacket turbine foundations ($n = 255$) or the transformer platform ($n = 30$). No fixes occurred on or near the gravity-based foundations. The individual proportion of time spent near the constructions compared with the total amount of time inside the wind farm varied strongly among the different birds, ranging from 0 to 100% and averaging at 33%.

The inner/outer turbine factor variable was found to have a significant effect (1.875 ± SE 0.447, $p < 0.001$, see Table A3 in Appendix) on the number of fixes per turbine buffer zone, which the model predicted to be 6.5 times higher at outer turbines. The model further predicted an exponential decrease in the number of fixes per turbine buffer zone with increasing distance to the coast (Figure 8). The model results are summarized in Appendix (Table A3).

Discussion

Using GPS telemetry data, this study investigated spatial patterns in the presence of lesser black-backed gulls in and around the Thornton Bank OWF. First, we estimated the effect of distance to the wind farm edge on lesser black-backed gull encounter rates. Non-flying birds seemed to avoid the inner part of the wind farm, with the number of fixes increasing up to a distance of 2 km, yet with a distinct secondary peak in presence right at the wind farm's edge. The latter was significantly explained by turbine presence inside the grid cells and therefore most probably represents birds resting on the outer turbine foundations. Close to the turbines, the majority (95%) of the gulls was indeed recorded as non-flying at a median height of 10 m above sea level. Note that outside the OWF, the registered height of offshore located non-flying gulls was strongly centred around zero (representing birds on the water). Moreover, lesser black-backed gulls were often observed perching on the turbine jacket foundations during ship-based monitoring surveys (Vanermen *et al.*, 2017). Flying birds too seemed to avoid the inner part of the wind farm and showed only slightly increased presence along the wind farm edge. The latter appeared independent of turbine presence and should be interpreted as an overall increase in flight activity along the borders of the wind farm. This may reflect a barrier effect and a corresponding accumulation of birds flying around rather than entering the wind farm (Desholm *et al.*, 2006), but might as well be due to local birds moving between the favoured outer turbines.

The fact that gulls concentrate on turbines along the wind farm edge is intriguing, as it points towards a conflict between the opposing forces of macro-avoidance of the wind farm as a whole and attraction towards individual turbines, where the birds are suspected to take advantage of the roosting or vantage point possibilities. Interestingly, unlike great black-backed (*L. marinus*) and herring (*Larus argentatus*) gulls, lesser black-backed gulls were never observed foraging on the intertidal fouling

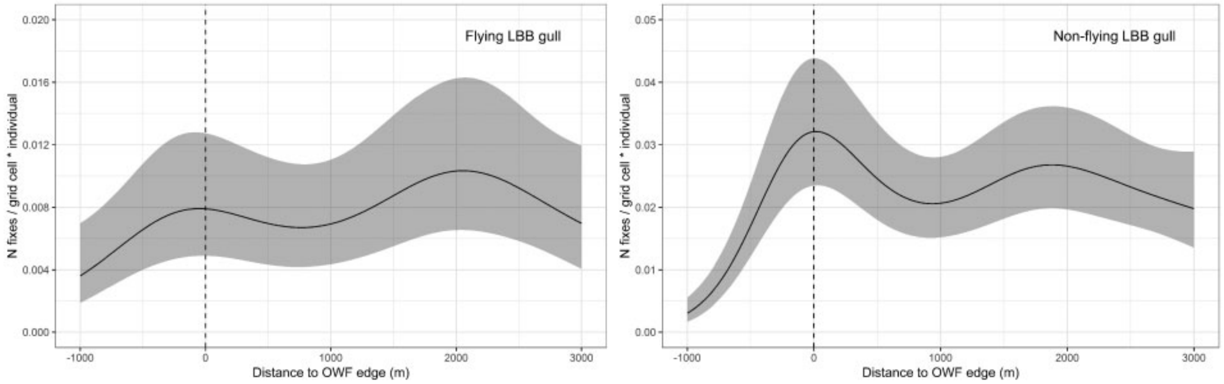

Figure 5. Model predictions of the effect of distance to the OWF edge on the number of fixes per 250 × 250 m grid cell and per individual for flying (left panel) and non-flying (right panel) lesser black-backed gulls showing the 95% confidence intervals.

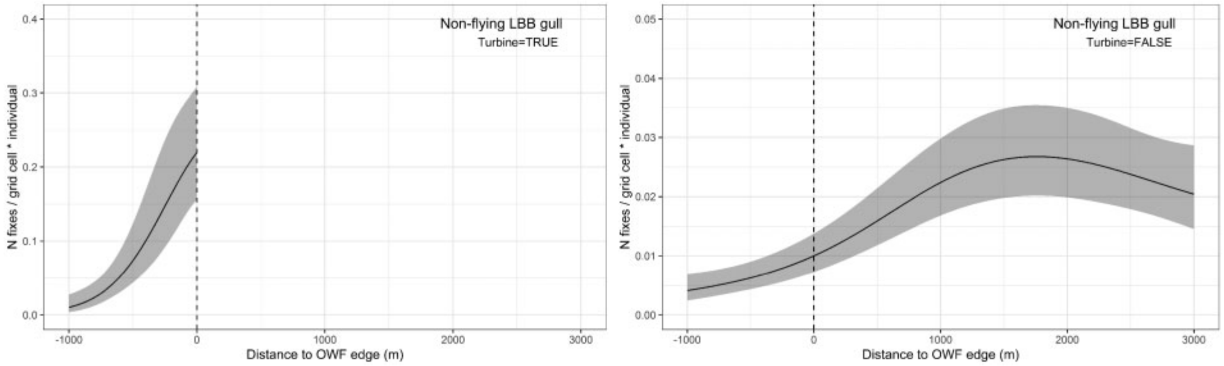

Figure 6. Model predictions of the effect of distance to the OWF edge on the number of fixes per 250 × 250 m grid cell and per individual for non-flying birds in turbine cells (left panel) and non-turbine cells (right panel) showing the 95% confidence intervals.

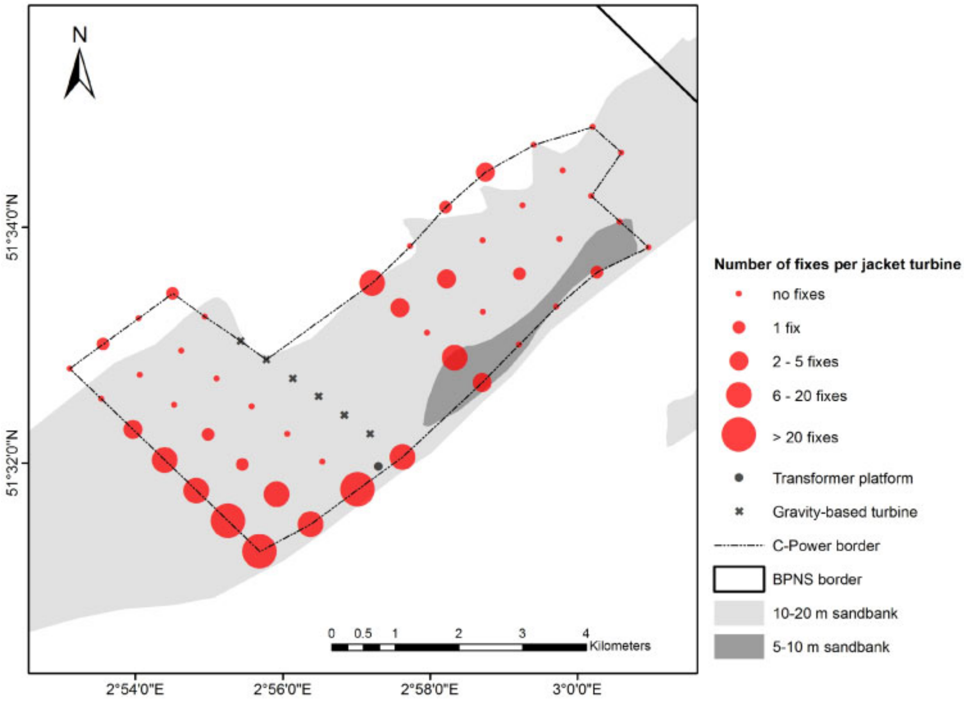

Figure 7. The number of GPS fixes of lesser black-backed gulls per jacket turbine (not analysed for turbines with a gravity-based foundation or for the transformer platform).

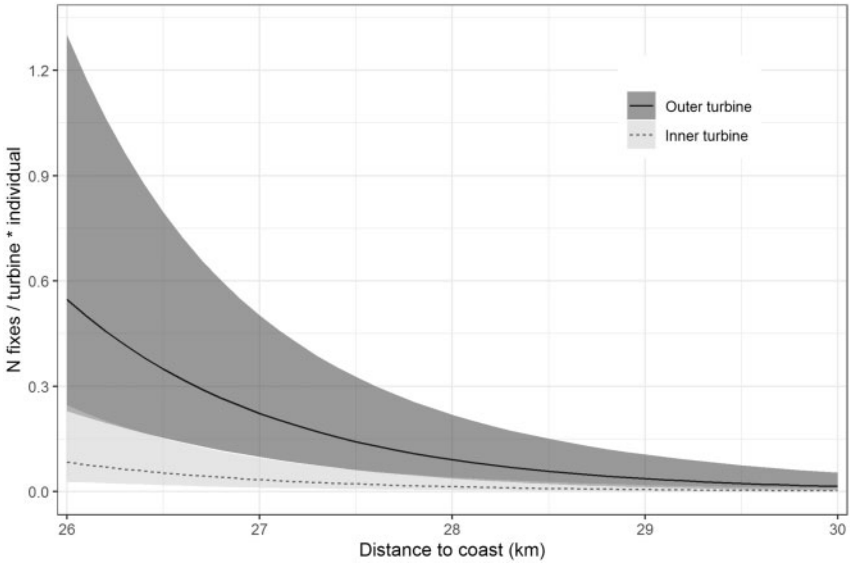

Figure 8. Model results for the number of GPS fixes per turbine and per individual in relation to distance to the coast (distinguishing between outer and inner turbines) showing the 95% confidence intervals.

communities of the foundations around low tide, at least not during Belgian ship-based monitoring campaigns, nor during observations with a fixed camera installed on one of the Thornton Bank turbine bases (Vanermen *et al.*, 2017). This, together with the avoidance of the wind farm interior of both flying and non-flying birds, counters the hypothesis of OWFs attracting lesser black-backed gulls because of increased food availability arising from artificial reef effects on and around the turbine foundations (e.g. Drewitt and Langston, 2006; Reubens *et al.*, 2014; De Mesel *et al.*, 2015), or alternatively, from an increase in benthic productivity or abundance of pelagic fish due to the absence of fisheries inside wind farms (e.g. Coates *et al.*, 2016).

In contrast to the results of before-after control-impact (BACI) analyses of at-sea surveys suggesting no displacement effect (Vanermen *et al.*, 2016, 2017), we observed a lower presence of lesser black-backed gulls inside the Thornton Bank OWF based on GPS telemetry data. There are, however, a number of aspects that have to be considered when interpreting or comparing these results. In the BACI analyses no distinction was made between age groups, while the GPS tracking analysis focused on adult birds only. One possible explanation for the diverging study outcomes could therefore be that young birds respond differently towards offshore wind turbines compared with adult individuals. Not bound to the coastal colony, immature birds can for example be expected to spend more time at sea and to habituate to wind farm presence more easily. Also, unlike the BACI monitoring, the analysis presented here is limited to the wind farm area and its near surroundings and the yet available tracking data do further not allow taking account of the reference situation before wind farm construction. Interestingly, the current construction of the Norther wind farm just southeast of the Thornton Bank will offer the unique opportunity to perform a before-after comparison of the distribution of tracked lesser black-backed gulls in and around an OWF site, provided a comparable tagging effort of lesser black-backed gulls in the colonies of Zeebrugge and Ostend is ensured. As this site is closer to the colonies this may also generate more data as well as additional opportunities, for example, to study barrier effects on commuting birds.

As opposed to a disturbance response, an alternative interpretation of the observed avoidance patterns in this study could be related to the role of fisheries, which are known to attract large numbers of gulls (e.g. Garthe *et al.*, 1996; Sotillo *et al.*, 2014). As fishing vessels are not allowed to trawl inside the wind farms, the low presence of lesser black-backed gulls in the wind farm interior might as well be due to “passive” avoidance resulting from the absence of fishery (Leopold *et al.*, 2013).

In a next step, we explored the gulls’ association with the jacket turbine foundations, at which tagged individuals spent half of their time when inside the wind farm. Considering the huge difference in surface between the 100 m turbine buffer areas and the OWF footprint area (respectively, 1.5 and 36.3 km^2) this indicates an unmistakable and strong attraction towards the turbines, at least once the birds are inside the wind farm boundaries. Modelling the number of fixes per turbine showed that the tracked gulls strongly preferred turbines along the wind farm edge, especially those oriented towards the coast and the study colonies. It should further be noted that the Thornton Bank wind farm consists of two clusters of turbines, with a 1700 m wide corridor in between. While the jacket turbines bordering this corridor were regarded as “inside” the wind farm in this exercise, the gulls clearly spent more time on these compared with other “inside” turbines (Figure 7). From the perspective of a lesser black-backed gull, the standard space between the turbine rows of 800–900 m thus seemed to be much less attractive to cross or enter compared with the 1700 m corridor, which created another favourable edge condition.

Limitations and considerations

The sub-sampling as used in this study is an often applied approach to overcome autocorrelation between subsequent fixes (e.g. Ross-Smith *et al.*, 2016; Shamoun-Baranes *et al.*, 2017;

Thaxter *et al.*, 2018), as well as a necessary step in this particular study in order to obtain a balanced and unbiased dataset considering the nature of our response variable (i.e. the number of fixes). Yet by discarding a large amount of data, we might lose valuable information. According to Fleming *et al.* (2017), autocorrelation itself should be thought of as a central and informative statistical characteristic of animal movement. Our approach could thus be taken forward by performing more advanced analyses, applying for example continuous-time movement models, particularly fit for analysing animal movement data (Calabrese *et al.*, 2016; Fleming *et al.*, 2017). Furthermore, it could be interesting to include year, breeding status or colony either as fixed or as random effects, to assess their effect on the within-OWF spatial use of lesser black-backed gulls or alternatively to account for possible dependancy. Regarding the latter it should be noted that including bird identity (the most important source of suspected pseudo-replication) as a random intercept into our models had little influence on the targeted smoothers and their corresponding significance levels. OWFs located closer to the colony of origin, ideally at a distance of less than 10 km, are likely to generate more GPS fixes in and around the area of interest, thus allowing to include additional variables. Fishery activity, assessed through the inclusion of vessel monitoring system (VMS) data, is yet another aspect which could be accounted for. Lastly, bird behaviour could be assessed in more detail by making use of the accelerometer incorporated in the UvA-BiTS trackers and designed to monitor body movement as well as temperature and barometric pressure (Bouten *et al.*, 2013).

Conclusion

In conclusion, on top of the known variation in the response of lesser black-backed gulls towards OWFs as a whole, ranging from avoidance to attraction depending on the study site (Dierschke *et al.*, 2016; Vanermen and Stienen, 2019), here we illustrated how spatial use may vary substantially within a single wind farm, interpreted as a meso-scale response pattern. This insight is of particular value to collision risk modelling (Band, 2012), as it highlights the necessity to take in account within-OWF variability in bird movements and presence, opposed to the assumption of a constant bird flux across the entire wind farm.

An increased understanding of the ecological incentives underlying such patterns in spatial use is a crucial step towards more reliable predictions of OWF impact on lesser black-backed gulls (and other large gulls *Larus* sp.) throughout their distribution range. Roosting opportunities, distance to the colony, wind farm configuration, local habitat as well as species characteristics are all suspected to explain at least part of the pattern observed at the Thornton Bank. Research at other wind farms on a range of large gull species is thus needed to reveal the extent as well as the causes of variation in meso-scale response patterns. This in turn would provide more widely applicable and much-needed input for (cumulative) wind farm impact assessments involving large gulls, a species group reported to be particularly sensitive to collision mortality (Furness *et al.*, 2013).

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Appendix

Table A1. Coefficient estimates for the models on the effect of distance on the number of ‘flying’ fixes: (a) $N_{1(\text{flying})} \sim D_{\text{coast}} + \text{s}\ (D_{\text{owf}}, k = 6)$ – Poisson model (AIC = 5158.1) and (b) $N_{1(\text{flying})} \sim D_{\text{coast}} + \text{s}(D_{\text{owf}}, \text{by} = TB_{\text{pres/abs}}, k = 6)$ – Poisson model (AIC = 5158.3).

(a)	**Estimate**	**Std. error**	***Z*-value**	**Pr(>|z|)**
(Intercept)	2.682	0.569	4.717	<0.001
D_{coast}	−0.279	0.020	−13.846	<0.001
	Edf	**Ref.df**	**Chi square**	***P*-value**
$\text{s}(D_{\text{owf}})$	4.428	4.846	22.15	<0.001
(b)	**Estimate**	**Std. error**	***Z*-value**	**Pr(>|z|)**
(Intercept)	2.666	0.569	4.685	<0.001
D_{coast}	−0.279	0.020	−13.844	<0.001
	Edf	**Ref.df**	**Chi. square**	***P*-value**
$\text{s}(D_{\text{owf}})\text{:as.factor}(TB_{\text{pres/abs}}) = 0$	4.214	4.724	21.196	0.001
$\text{s}(D_{\text{owf}})\text{:as.factor}(TB_{\text{pres/abs}}) = 1$	1.794	2.015	4.158	0.127

Table A2. Coefficient estimates for the models on the effect of distance on the number of ‘non-flying’ fixes: (a) $N_{1(\text{non-flying})} \sim D_{\text{coast}} + \text{s}\ (D_{\text{owf}}, k = 6)$ – negative binomial model (AIC = 10772.1) and (b) $N_{1(\text{non-flying})} \sim D_{\text{coast}} + \text{s}(D_{\text{owf}}, \text{by} = TB_{\text{pres/abs}}, k = 6)$ – negative binomial model (AIC = 10348.6).

(a)	**Estimate**	**Std. error**	***Z*-value**	**Pr(>|z|)**
(Intercept)	4.092	0.404	10.12	<0.001
D_{coast}	−0.294	0.014	−20.39	<0.001
	Edf	**Ref.df**	**Chi square**	***P*-value**
$\text{s}\ (D_{\text{owf}})$	4.819	4.983	65.14	<0.001
(b)	**Estimate**	**Std. error**	***Z*-value**	**Pr(>|z|)**
(Intercept)	3.529	0.386	9.139	<0.001
D_{coast}	−0.281	0.014	−20.364	<0.001
	Edf	**Ref.df**	**Chi square**	***P*-value**
$\text{s}\ (D_{\text{owf}})\text{:as.factor}\ (TB_{\text{pres/abs}}) = 0$	3.507	4.142	112.3	<0.001
$\text{s}\ (D_{\text{owf}})\text{:as.factor}\ (TB_{\text{pres/abs}}) = 1$	2.534	2.803	436.9	<0.001

Table A3. Coefficient estimates for the model on turbine association.

	Estimate	**Std. error**	***Z*-value**	**Pr(>|z|)**
$N_2 \sim D_{\text{coast}} + TB_{\text{inner/outer}}$ – negative binomial model				
(Intercept)	20.852	4.485	4.650	<0.001
as.factor $(TB_{\text{inner/outer}})$=outer	1.875	0.447	4.192	<0.001
D_{coast}	−0.897	0.165	−5.434	<0.001