RESEARCH ARTICLE



Avian vulnerability to wind farm collision through the year: Insights from lesser black-backed gulls (*Larus fuscus*) tracked from multiple breeding colonies

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Abstract

- Wind energy generation has become an important means to reduce reliance on fossil fuels and mitigate against human-induced climate change, but could also represent a significant human-wildlife conflict. Airborne taxa such as birds may be particularly sensitive to collision mortality with wind turbines, yet the relative vulnerability of species' populations across their annual life cycles has not been evaluated.
- 2. Using GPS telemetry, we studied the movements of lesser black-backed gulls Larus fuscus from three UK breeding colonies through their annual cycle. We modelled the distance travelled by birds at altitudes between the minimum and maximum rotor sweep zone of turbines, combined with the probability of collision, to estimate sensitivity to collision. Sensitivity was then combined with turbine density (exposure) to evaluate spatio-temporal vulnerability.
- 3. Sensitivity was highest near to colonies during the breeding season, where a greater distance travelled by birds was in concentrated areas where they were exposed to turbines.
- 4. Consequently, vulnerability was high near to colonies but was also high at some migration bottlenecks and wintering sites where, despite a reduced sensitivity, exposure to turbines was greatest.
- 5. Synthesis and applications. Our framework combines bird-borne telemetry and spatial data on the location of wind turbines to identify potential areas of conflict for migratory populations throughout their annual cycle. This approach can aid the wind farm planning process by: (a) providing sensitivity maps to inform wind farm placement, helping minimize impacts; (b) identifying areas of high vulnerability where mitigation warrants exploration; (c) highlighting potential cumulative impacts of developments over international boundaries and (d) informing the conservation status of species at protected sites. Our methods can identify pressures and linkages for populations using effect-specific metrics that are transferable and could help resolve other human-wildlife conflicts.

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KEYWORDS

bird, collision risk, GPS telemetry, human-wildlife conflict, renewable energy, sensitivity, vulnerability, wind turbine

1 | INTRODUCTION

The need to mitigate for human-induced climate change led to political consensus at the 21st Conference of Parties of the UNFCCC, where delegates agreed to stem further increases in global temperatures below 2°C, with concerted effort to limit increases to 1.5°C (UNFCCC, 2015). To meet such targets, many countries are investing in low emission renewable energy technologies, of which wind energy is a cost-effective and well-developed means of electricity generation (Kumar et al., 2016). However, wind farms could negatively impact biodiversity, ecosystems and populations of protected species (Schuster, Bulling, & Köppel, 2015), resulting in an urgent need to appraise the potential vulnerability of species.

A key effect of wind farms on airborne taxa such as birds and bats is collision mortality (Drewitt & Langston, 2006). Many migratory species especially can cover large distances through the year, crossing international boundaries (Baerwald, Patterson, & Barclay, 2014). As such, there is a need to understand the linkages between specific populations of interest (such as protected breeding populations) and areas of high development where pressures may exist. While there has been a focus on impacts to protected site populations during the breeding season (Pearce-Higgins, Stephen, Langston, Bainbridge, & Bullman, 2009), some species of birds (Carrete, Sanchez-Zapata, Benitez, Lobon, & Donazar, 2009) and bats (Zimmerling & Francis, 2016) may be at risk of impacts at other times of the year as well. Wind farm interactions can be informed by likely dispersal and movement patterns of species, for example using mark-recapture ringing data for birds (Furness, 2015). However, these data may be at coarse spatial scales and unable to determine the precise provenance of individuals and populations at risk. Recent studies have used tracking telemetry to assess overlaps between the habitat or area used by species and developments (Mojica, Watts, & Turrin, 2016; Reid, Kruger, Whitfield, & Amar, 2015; Singh et al., 2016; Wade et al., 2014; Watson, Duff, & Davies, 2014), making it an effective way of evaluating wildlife-wind farm interactions for specific populations.

These challenges are particularly difficult for migratory species, which may be vulnerable to collision during the breeding season, on migration and at non-breeding locations (Thaxter et al., 2017). The populations of many migratory bird species have declined markedly in recent decades, particularly for seabirds (Birdlife International, 2018; Paleczny, Hammill, Karpouzi, & Pauly, 2015), linked to threats such as fisheries, invasive species and renewable energy developments. Given the conservation concern for these populations and the current and likely future magnitude of wind farm developments globally, including where migrants are concentrated (Thaxter et al.,

2017), there is an urgent need to develop approaches to robustly assess their vulnerability to collision with turbines. This requires good information about the location and movements of species through their annual life cycle. The vulnerability of species to collision through the year, however, has not been examined.

Key determinants of collision risk include flight altitude relative to the vertical sweep of turbine blades, avoidance behaviour, speed of movement and temporal use of an area (Masden & Cook, 2016). Previous studies on marine bird species have used these metrics to produce indices of potential sensitivity to wind farm development (Furness, Wade, & Masden, 2013), that when combined with at-sea survey data, can generate spatial maps of species' sensitivity (Bradbury et al., 2014). Tracking telemetry offers a practical way of gathering distribution data for specific populations (Cleasby et al., 2015; Reid et al., 2015). Telemetry can identify linkages between populations and developments, and provide information on determinants of collision risk. Moreover, tracking birds from different colonies of the same species could determine the relative importance of threats from anthropogenic pressures in different parts of the species' range. Yet telemetry-based approaches to estimating sensitivity are uncommon, and when combined with where a species may be exposed to collision risk, such as the distribution of wind turbines, could be used to map vulnerability (Appendix S1).

Among seabirds, the lesser black-backed gull Larus fuscus is considered vulnerable to collision with terrestrial and offshore wind turbines (Furness et al., 2013; Thaxter et al., 2017). Lesser black-backed gulls are known to enter offshore wind farms (Thaxter et al., 2018) and a relatively high proportion (c. 34%) of individuals may fly at turbine height (Johnston, Cook, Wright, Humphreys, & Burton, 2014; Ross-Smith et al., 2016). This species is of conservation concern, listed under Annex 1 of the EU Birds Directive (2009/147/EC) and of Amber status in the list of Birds of Conservation Concern in the UK, Channel Islands and Isle of Man (Eaton et al., 2015) due to the international importance, and concentration, of its breeding population at protected site colonies, where there have been significant recent declines (Ross-Smith et al., 2014). Although offshore wind farms close to breeding colonies may pose a risk to breeding birds, lesser black-backed gulls frequently use inland habitats (Thaxter et al., 2018) and may travel hundreds of kilometres from breeding sites to wintering destinations (Klaassen, Ens, Shamoun-Baranes, Exo, & Bairlein, 2012; Shamoun-Baranes, Burant, van Loon, Bouten, & Camphuysen, 2017). Consequently, in common with other migratory species, lesser black-backed gulls may be vulnerable to developments far from breeding colonies in ways that may not be obvious to regulatory authorities responsible for approving wind farms. A

complete trans-boundary assessment of potential conflicts with wind farms through the year and across all habitats is therefore necessary.

To address this issue, we tracked the annual movements of lesser black-backed gulls from three colonies that, at the time of the last census, supported 30% of the UK and Irish breeding population (Mitchell, Newton, Ratcliffe, & Dunn, 2004). We modelled the distance travelled (combining flight speed and temporal use) within a spatially bespoke collision risk window (flight altitude of birds within the minimum and maximum rotor sweep zone), combining this with probability of collision (Band, 2000), to approximate sensitivity to collision risk. This sensitivity surface was combined with the density of wind turbines, that is 'exposure' to wind farms, to estimate spatiotemporal 'vulnerability'.

2 | MATERIALS AND METHODS

2.1 | Capture and attachment of GPS devices

Fieldwork was conducted at three UK colonies within Special Protection Areas (EC Birds Directive 2009/147/EC), where breeding lesser black-backed gulls are a designation feature: Orford Ness (52°4′N, 1°33′E), South Walney (54°40′N, 3°14′W), hereafter 'Walney', and Skokholm (51°41′N, 5°16′W) (Appendix S1). Solar-powered Global Positioning System (GPS) tags (University of Amsterdam Bird-Tracking System, Bouten, Baaij, Shamoun-Baranes, & Camphuysen, 2013) were attached to 25, 24 and 25 breeding adult lesser black-backed gulls at each site respectively (Table 1) to collect data on the geographical position and altitude of birds over the annual cycle. Tagging was undertaken under licence, approved by the independent Special Methods Technical Panel of the UK

Ringing Scheme. The total weight (device plus harness) was <21 g (<3.2% body mass, mean weights: Orford Ness, 851 \pm 85 g, range: 710–955 g; Walney, 813 \pm 100 g, range: 660–990 g; Skokholm, 798 \pm 89 g, range: 670–1,010 g; see Appendix S1 for details of tags and the system). Date-time stamped GPS locations were recorded every 5–10 min during the breeding season (*c.* May–August), and 30–60 min at other times of the year (Appendix S1).

3

2.2 | Data manipulation

We used data representing at least the first full year of tracking of each individual. At Orford Ness, 11 birds were tagged in 2010 and 14 in 2011, providing data from June 2010 to August 2011 and from May 2011 to August 2012 respectively (Appendix S2). For birds from Walney and Skokholm, data came from May 2014 to August 2015. Only birds that left the colony and returned the following year were included in analyses (Table 1). A full second breeding season was included to maximize data available for birds from Walney and Skokholm, necessitating a random effect of bird ID in analyses; this approach avoided spurious annual cut-offs for each bird.

We used a grid-based approach ($20 \times 20 \text{ km}$ grid squares, hereafter 'squares') to assess sensitivity and vulnerability to collision across the species' annual range. We initially investigated metrics identified as key determinants of collision risk (Masden & Cook, 2016), quantifying for each bird and square per day: (a) the intensity of area use, defined as the total time spent; (b) mean flight speed and (c) the proportion of time at collision risk height (Figure S1.1). Sensitivity (S) to collision for individual birds (S) was then estimated as a combined metric of these parameters (1–3) and the probability of collision. This was achieved by first combining the product of T (time spent, minutes), S (ground speed, m/s) and S (proportion of time at collision risk

TABLE 1 Sample sizes of birds tagged in each year cohort, and numbers of birds with data available during breeding and non-breeding periods; hyphens indicate no information gathered; 'Max' is the maximum number of birds providing data across all years

Colony	Cohort	Number tagged	Year	Breeding season data	Non-breed- ing data	Non-UK wintering destination	Wintering destination UK and non-UK	Wintering desti- nation UK only
Orford Ness	2010	11	2010	10	6ª	2	4	0
			2011	5 ^a	3	2	1	0
	2011	14	2011	14	12	0	7	5
			2012	12	10	0	5	5
			Max	24	18	2	11	5
Walney	2014	24	2014	24	16	3	7	6
			2015	16	-	_	_	_
			Max	24	16	3	7	6
Skokholm	2014	25	2014	25	20	9	8	3
			2015	20	_	_	_	_
			Max	25	20	9	8	3

Note: Non-breeding periods are split by birds departing directly overseas ('Non-UK'), departing overseas after remaining for a time in the UK ('UK and non-UK') and solely remaining in the UK. Sample sizes for the first full year of data per bird (used in analyses) are given in italics; Orford Ness: 18 birds (2010–11, n = 6; 2011–2012, n = 12), Walney: 16 birds (2014–15), Skokholm 20 birds (2014–15).

^aOne bird recovered during the 2010/11 non-breeding period providing no breeding season information the following year.

height, m) for each bird b, square i and day of the year j, equating to the distance (speed x time) travelled within the collision risk window (d):

$$d_{ij}^b = T_{ij}^b G_{ij}^b R_{ij}^b \tag{1}$$

The sensitivity index (S_{ij}) was then determined by summing d^b_{ij} across birds (D_{ij}) , reflecting the annual flux of birds per square (Figure 1) and multiplying this value by the probability of collision P_i :

$$S_{ij} = D_{ij}P_i, (2)$$

where $D_{ij} = \sum_{b=1}^{n} d_{ij}^{b}$.

The calculation of P_p was based on the Band (2000) collision model, using information on mean turbine characteristics per square. The proportion of time at collision risk height was calculated for bespoke collision risk windows (CRW) per square, based on the characteristics of wind farms operational or under construction at those locations. For this purpose, a point location dataset of wind farm locations was used (The Wind Power, 2015) to derive mean minimum and maximum blade tip heights above ground level (onshore) or mean sea level (offshore) per square representing CRW

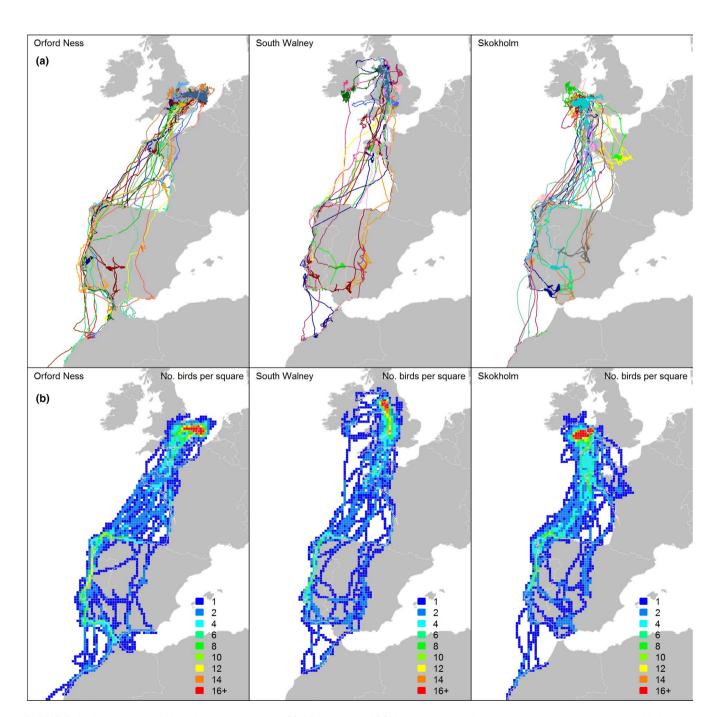


FIGURE 1 Movements of birds through the year as (a) GPS tracks and (b) the annual flux of movement, depicted as number of birds per square per year

boundaries. Where no wind farms occurred, mean CRWs were determined for onshore (41 \pm 14 to 116 \pm 26 m) and offshore (29 \pm 8 to 135 \pm 29 m) squares, based on mean lower and upper rotor sweep heights. Ground speed was used to distinguish flight (>4 km/hr) from other behaviours such as resting (\leq 4 km/hr; Shamoun-Baranes, Bouten, Camphuysen, & Baaij, 2011). A digital elevation model (Farr et al., 2007) was used to correct for topographical variations to derive altitude above ground surface for each GPS fix, allowing a standardized assessment across varying topography. Paths between GPS fixes were interpolated (to 10 s) to ensure complete coverage across the grid. The same wind turbine dataset above was also used to calculate the summed number of terrestrial and marine wind turbines per square, as an index of 'exposure' to intensity of wind farm activity (Section 2.3).

2.3 | Analysis

2.3.1 | Sensitivity

We used General Additive Mixed-effects Models (GAMMs) to draw out smoothed spatio-temporal patterns in the raw data and better approximate sensitivity (see Cleasby et al., 2015 for a similar approach; Appendix S3). For each colony, $d_{ij}^{\rm b}$ (Equation 1), was modelled across birds to provide the surface D_{ij} :

$$D_{ij} = s \left(x_i y_i, j_i \right) + r \left(b \right) + \varepsilon_{ij}$$
 (3)

An isotropic smooth term (s) for the mid-point longitude and latitude coordinates (x and y) of squares (i) was allowed to vary by Julian date (j), as a circular variable. Occasionally, gaps in the GPS data occurred when birds were at northerly latitudes (c. >45°N) during non-breeding, preventing sufficient solar charging of some tags. To help account for this, models were weighted by the inverse of the proportion of birds giving data (per day, square and year) from all 'active' tags within these latitudes (Appendices S2 and S3). This weighting acted as an imputation, to simulate D_{ii} should inactive tags had been active (Appendix S3). Models were specified using a Tweedie error (ε) distribution (Wood, 2006), deemed the best fitting model (index parameter, p = 1.2). A random term for bird ID r(b) was included to account for pseudo-replication. D_{ii} was then multiplied by P_i , to provide S_{ii} (Equation 2). A high degree of spatial and temporal resolution was specified by varying the kparameter as the dimension of the basis for the penalized regression smooth term (Wood, 2006). Due to computational limitations, two separate models for Equation (3) were specified (Appendix S2) representing: (A) fine-scale spatial resolution (space k = 200, time k = 5) used for assessing patterns over space; (B) fine-scale temporal resolution (space k = 25, time k = 100), for assessing patterns over time. Predictions were generated for all squares within the spatial range of birds from each colony, for all Julian dates. However, our models had low predictive power to estimate S_{ii} for areas not visited by birds (Appendix S3). To produce total surfaces across the year, model A predictions for each square and day (d_{ij}) were aggregated to give a value for each square across Julian dates (D_i) , where n = 365 days:

$$S_i = \sum_{i=1}^n S_{ij},\tag{4}$$

visualized as quantiles of the full range of predictions over squares, at defined percentage thresholds (Figure 2). To describe model error, we calculated the Relative Standard Error (RSE, standard error/mean) for each square. To produce finer-scale temporal trends, predictions of S_{ij} from model B were then summed across all squares i for each Julian date i (Appendix S2):

$$S_{j} = \sum_{i=1}^{n} S_{ij}, \tag{5}$$

where n is the total number of squares for each colony.

2.3.2 | Vulnerability

For models A and B Equation (3), sensitivity S_{ij} was multiplied by 'exposure' (number of wind turbines per square, T_i), to generate a vulnerability index value (v_{ii}) for each square per day:

$$V_{ij} = S_{ij}T_i \tag{6}$$

Final aggregated spatial and temporal vulnerability surfaces then followed as:

$$V_i = \sum_{j=1}^n V_{ij} \tag{7}$$

$$V_j = \sum_{i=1}^n V_{ij} \tag{8}$$

For temporal presentation of predictions through Equation (8), the daily summed vulnerability indices V_j for model B were divided by the number of prediction squares for each colony to represent a mean and variation (±1 standard error, SE) across squares, scaled from 0 to 1 in relation to the maximum value per square across the ij matrix. These analyses therefore compared variations in distributions of sensitivity and vulnerability between colonies. To investigate annual cross-colony sensitivity (\bar{S}_i) and vulnerability (\bar{V}_j), S_i and V_j were aggregated across colonies (c) and further weighted by colony size (\dot{P}_c ; Appendix S1):

$$\bar{S}_i = \sum_{c=1}^n \left(S_{ci} \dot{P}_c \right) \tag{9}$$

$$\bar{V}_i = \sum_{c=1}^n \left(V_{ci} \dot{P}_c \right) \tag{10}$$

To avoid biases due to uneven numbers of tagged birds at each colony, aggregations were performed on scaled probability

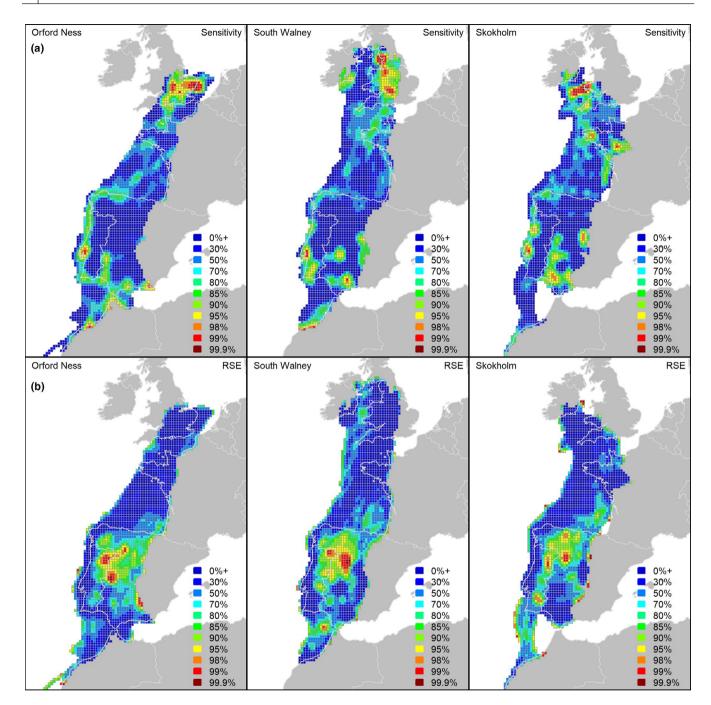


FIGURE 2 Modelled surfaces for birds from Orford Ness, Walney and Skokholm showing (a) relative distance travelled within the collision risk windows indicative of sensitivity (presented as quantiles of model predictions) and (b) Relative Standard Error (RSE) for all surfaces

surfaces as defined above. Temporal vulnerability scores were examined in relation to stages of the annual cycle across the year (Klaassen et al., 2012) defined by: (a) departure from the nest site, (b) return the following spring, and for birds leaving the UK during the non-breeding period, (c) departure from last UK roost/stopover site (autumn migration), (d) arrival at first wintering site and (e) departure from last wintering site (spring migration; Table 1; Appendix S1). Data manipulation and mapping were conducted using R 3.5.0 (R Core Team, 2018), and spatial analyses using R package 'mgcv' (Wood, 2006).

3 | RESULTS

3.1 | Migratory strategy

A total of 11%, 19% and 45% birds that provided data for a full year of tracking from Orford Ness, Walney and Skokholm left the UK directly after the breeding season for overseas destinations (Table 1). Other birds that left the UK did so after remaining in the UK for part of the non-breeding period (61%, 44% and 40% of birds from Orford Ness, Walney and Skokholm, respectively, Table 1). The remaining proportions

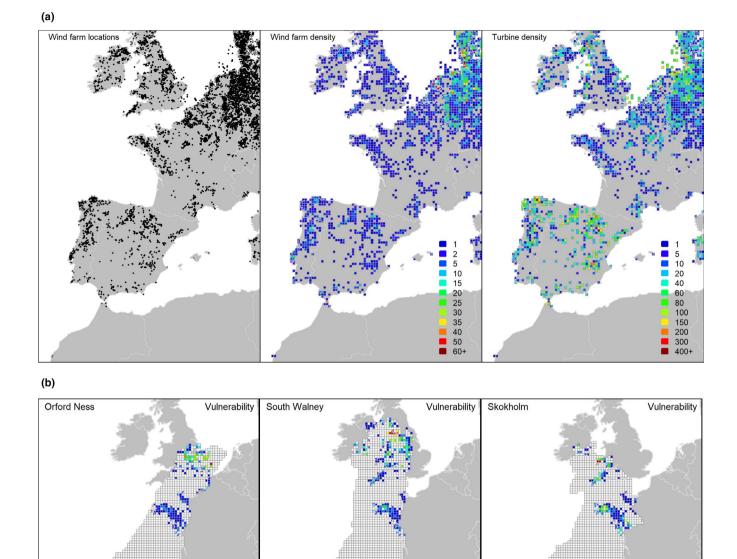


FIGURE 3 (a) Distribution and gridded summaries of the geographical point locations of wind farms, the number of wind farms per square and number of turbines per square; (b) annual vulnerability per square (presented as quantiles of annual vulnerability predictions), for Orford Ness, South Walney and Skokholm

of birds (28%, 38% and 15% respectively) remained in the UK through the year (Table 1, Table S1.1). However, the proportions of birds adopting the three strategies were not significantly different between colonies ($\chi_4^2 = 7.51, p = .10$). Migration corridors for each colony were clearly defined (Figure 1). Overseas destinations included Portugal, central/southern Spain, northern/western Morocco (all colonies), Mauritania (Orford Ness), northern France (Skokholm) and Ireland (Walney).

30%

50%

70%

80%

85%

90%

95%

98%

99.9%

3.2 | Sensitivity to collision

0% >0%+

30%

50%

70%

80%

85%

90%

95%

98%

99%

99.9%

Results suggested good model performance for each colony (deviance range for model A: 50.6%–62.4%, and model B: 44.4%–56.3%, Table S2.1). Faster flight speeds were recorded over oceans and higher flight altitudes inland (Figure S1.1). Models therefore revealed significant spatio-temporal variation distances travelled in the CRW

30%

50%

70%

80%

85%

90%

95%

98%

99.9%

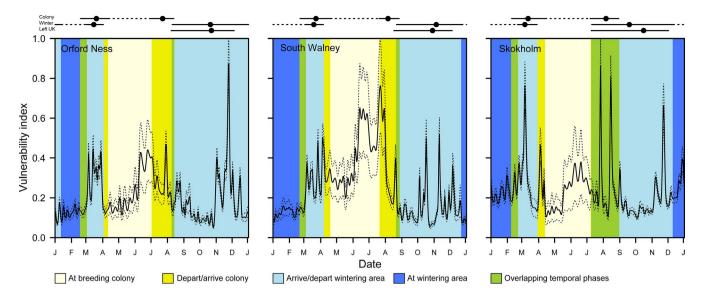


FIGURE 4 Mean temporal trends in potential vulnerability (mean daily summed vulnerability predictions per square scaled to a maximum of 1.0) across the year for birds from Orford Ness, Walney and Skokholm (±1 SE representing variation across squares). Phases of the annual cycle are shown. Distribution of dates for movements to and from the 'colony', 'winter' sites, and for when birds 'left UK' are provided, expressed as solid lines (range), filled circles (median) and dashed lines (intervening periods); 'overlaps' between phases, for example where some birds arrived at wintering areas but others were still in transit, are also shown

between individuals from each colony (p < .001 in all cases, Table S2.1). Comparing sensitivity maps for each colony indicated similarities in hotspots, evident around breeding colonies and wintering areas, as well as inland areas along flyways for each colony (Figure 2). Greatest model uncertainty (RSE) was recorded towards the edges of the prediction grid and areas used infrequently, primarily on the Iberian Peninsula (Figure 2).

3.3 | Vulnerability to collision

During breeding, a greater concentration of birds travelled further within the CRW in squares with high wind turbine density, resulting in high vulnerability to collision in areas near to colonies (Figures 3 and 4). This pattern was most notable for birds from Walney that used offshore areas containing high densities of turbines, reflected in a peak in vulnerability during breeding (Figure 4). For birds from Skokholm, vulnerability near the colony was high due to the presence of onshore turbines. The northern coasts of Spain and Portugal were primarily used for a limited time during migration; however, Galicia (Spain) contains a relatively high density of onshore wind turbines (maximum/square, 473 turbines), resulting in high vulnerability predictions in this area, comparable to peaks during breeding (Figures 3 and 4). Further clusters of high vulnerability were seen at the wintering destinations of birds (Figure 3). Consequently, the vulnerabilities of birds during the non-breeding season were, at times, comparable or higher than those for the breeding period (Figure 4).

3.4 | Combined colony patterns

Aggregating surfaces indicated shared sensitivity hotspots in the UK, along the Portuguese coast and southern Spain (Figure 5).

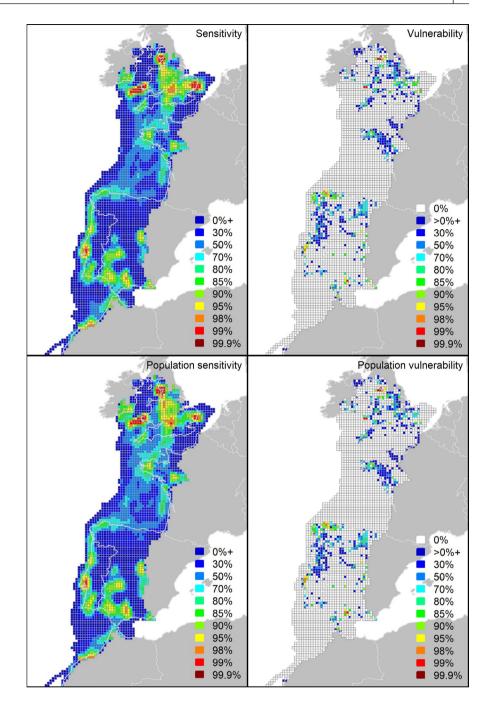
Vulnerability close to breeding colonies was most apparent for birds from Walney and Skokholm, particularly when weighted by colony size (Orford Ness being the smallest colony, Appendix S1). Birds from Orford Ness also had the lowest absolute mean vulnerability across the year, and those from Walney the highest (Appendix S3).

4 | DISCUSSION

4.1 | Sensitivity and vulnerability of lesser blackbacked gulls to collision

By tracking individual lesser black-backed gulls, we quantified the sensitivity and potential vulnerability of this species to wind turbine collision through their annual cycle. This is the first time that such an assessment has been undertaken for a migratory species. By doing so across three colonies representing nearly a third of the UK and Irish breeding population (Mitchell et al., 2004), we show qualitatively that patterns of sensitivity and vulnerability were broadly similar between them. However, localized differences were also evident, dependent on precise migratory paths, wintering locations and exposure to wind turbines near to breeding colonies. Importantly, individuals were not only vulnerable to collision during the breeding season from wind farms in the proximity of breeding colonies, but may also be vulnerable during non-breeding periods from wind turbines located far away from breeding colonies. Sensitivity and vulnerability to collision was high during breeding, when adults are restricted to central place foraging, and movements are concentrated into a relatively small area. However, vulnerability also showed peaks of similar magnitude across the non-breeding period, despite a smaller overall sensitivity. Vulnerability was high in Galicia on migration,

vulnerability per square (presented as quantiles of summed annual vulnerability predictions), for Orford Ness, South Walney and Skokholm combined, depicted as both individual colony sensitivity and vulnerability (equal weighting for each colony, top row) and at the 'population' level weighting surfaces (bottom row) by the overall population size at each colony



and wintering areas such as Lisbon and Malaga (Figure 5), due to a greater likely exposure to the effect of collision. Galicia has been an area of significant exploitation of wind energy in Europe (Tapia, Dominguez, & Rodriguez, 2009) and has one of the highest wind farm energy regional outputs in Spain (The Wind Power, 2015).

Wind farms could have significant meta-population impacts for species with large home-ranges (Carrete et al., 2009). Therefore, approaches that consider the full range of areas and habitats that species use through the year are crucial to identifying potential impacts on populations. Previous studies have mapped risk during migration (Mojica et al., 2016), winter (Pearse, Brandt, & Krapu, 2016) or breeding (Singh et al., 2016; Watson et al., 2014), however, ours

appear to be the first that does so across the annual cycle. A recent trait-based assessment of species' collisions with onshore wind turbines revealed that, on balance, migratory bird and bat species may be more at risk of collisions than more sedentary resident species (Thaxter et al., 2017). Many seabirds are migratory and, as *k*-selected species characterized by low fecundity and late maturity, will also be most sensitive to the impact of additional mortality from wind farms (Niel & Lebreton, 2005; Sæther & Bakke, 2000). Our study, however, did not aim to assess population-level effects, which would require demographic modelling (Beston, Differndorfer, Loss, & Johnston, 2016). With an increasing number of species being tracked (Bridge et al., 2011), our study demonstrates how such data can be used for a clear, applied conservation purpose, to inform assessments

of vulnerability to wind farm collision across the annual life cycle. Importantly, by doing so, we have identified what might be regarded as otherwise cryptic sources of potential mortality both between and among different breeding populations at sites located thousands of miles away from those colonies.

Lesser black-backed gulls in this study were highly variable in their migratory strategy, and as a species have become increasingly more sedentary since the mid-twentieth century (Newton, 2007). Nevertheless, the high vulnerability identified in parts of the flyway is of conservation concern. Fine-scaled assessment of mortality where vulnerability is greatest would therefore be valuable. Given ongoing changes in the migratory behaviour of a range of species, for example due to changes in land management or climate change, GPS tracking technologies provide a robust and rapid way of assessing the migratory routes and collision risk of individuals from populations. Although there are challenges in incorporating potential impacts of wind farms far removed from protected breeding colonies within assessments, particularly across national or international boundaries, our study outlines a way for such data to be gathered, that could be widely applied.

4.2 | Limitations

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Despite these advances, our study has some limitations. First, the resolution of the analysis (20 × 20 km) could have over-emphasized vulnerability in coastal grid squares where movements of birds were restricted to the coast, but where wind farms were located on inland hills and ridges or offshore. Conversely, at the scale of wind farms, effects could be underestimated if taking information from the wider area. The movements of birds in coastal grid squares were not restricted to the coast, hence we do not think the grid-based methodology and scale produced spurious results, but finer-resolution analyses for particular hotspots would improve accuracy. Our results are most useful for approximating wider-scale vulnerability rather than demonstrating connectivity to specific wind farms. Some further limitations are common to studies of impacts at individual wind farms, but were not addressed here due to the continental scale of the analysis. These include, secondly, the sensitivity surface presented, which although related to factors rendering a species more vulnerable to collision, is partly reflective of the flux of movement through an area. A previous study, however, has shown that collision rates do not necessarily increase linearly in relation to densities (de Lucas, Janss, Whitfield, & Ferrer, 2008), and as such the location of our vulnerability hotspots may not necessarily equate to maximal impacts. Third, the spacing, size and layout of individual wind farms will also play a part in collision risk, although our final calculation of vulnerability incorporated rotor length and turbine speed within the probability of collision. Fourth, our study did not assess population-level effects or account for habituation to wind farms (Appendix S1). This could be investigated through tracking studies (Garthe, Markones, & Corman, 2017), but would require finescaled approaches, covering pre-construction and operational

periods of developments to investigate behavioural changes (e.g. flight altitude or avoidance, Thaxter et al., 2018). Fifth, our tracking data had occasional data gaps during non-breeding periods; although these were partly handled through sensitivity modelling, this may have resulted in underestimation of the use of UK overwintering locations. Finally, our GPS-derived altitude estimates had measurement errors that could influence interpretation of overlaps with CRWs. However, the distributions of flight altitudes were comparable with those reported by Ross-Smith et al. (2016), where such errors were incorporated, and thus are considered representative.

4.3 | Implications for management and conservation

Our findings can inform the management and conservation of species in several ways. First, our sensitivity maps may be useful to inform the siting of wind farms, for example within larger-scale strategic environmental assessment (SEA). Assessments of sensitivity have generally been based upon concentrations of bird abundance and occurrence (Bright et al., 2008). Although these methods rarely consider the movements of individuals (BirdLife International, 2018; Reid et al., 2015), the approaches can be analogous; for instance our approach that treated tracking data observations independently would likely yield similar results to survey-based sensitivity assessments, but are specific to the populations studied. For migratory species, limiting the development of wind farms in areas that have bottlenecks, or along important flyways for sensitive species, is an important strategy for minimising impacts on biodiversity (Thaxter et al., 2017). Our approach provides a powerful way of informing SEA across a flyway, assessments which are urgently needed (CMS, 2017), while identifying areas where further study might be warranted, for example within impact assessments. Second, our vulnerability maps can help identify areas where the collision risk at operational wind farms may be greatest for particular populations, and where mitigation measures could be explored, such as adjusting cut-in speeds of turbines (Arnett, Huso, Schirmacher, & Hayes, 2011) and defining turbine shut-down periods (de Lucas, Ferrer, Bechard, & Muñoz, 2012). Third, our study highlights the importance of considering cumulative impacts of developments on species' populations. Understanding linkages between protected populations and areas of high sensitivity, and potential effects of developments on multiple populations, is of prime importance for ensuring renewable energy development takes place in a sustainable manner. Lastly, assessing through-the-year vulnerability facilitates better understanding of the risks that different populations may face, and can therefore help inform the conservation status of feature species at designated sites.

Maps of sensitivity and vulnerability to wind farms can be constructed from a variety of datasets (Birdlife International, 2018; Bradbury et al., 2014; Bright et al., 2008; Noguera, Perez, & Minguez, 2010; Thaxter et al., 2017). Bird-borne telemetry offers an alternative and complementary means of scoping areas of

potential conflict across the annual cycle, combining elements of behaviour specifically relevant to collision risk modelling (Cleasby et al., 2015; Masden & Cook, 2016). Our methods are transferable for use on other mobile taxa where human-wildlife conflicts may exist. The majority of bird species most vulnerable to wind turbine collision are large raptors, migratory soaring birds, as well as some species of seabird (Thaxter et al., 2017). Long-life GPS tags may be suitable for deployment on other potentially vulnerable species that, through our approach, would benefit from mapping of migratory routes and hotpots of vulnerability. With an ever-expanding global renewable energy footprint, methods that employ a comprehensive approach towards the conservation of species throughout their range and annual cycle such as these are sorely needed.

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AUTHORS' CONTRIBUTIONS

C.B.T. conducted the analyses and wrote the manuscript, N.H.K.B., C.B.T., V.H.R.-S. and W.B. designed the study, V.H.R.-S., N.A.C., G.J.C., G.D.C., L.J.B. and C.B.T. conducted fieldwork, E.A.M. provided additional hardware and W.B. facilitated inception and collaboration of the study through UvA-BiTS. All inputted to the manuscript and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data available via the Dryad Digital Repository https://doi.org/10.5061/dryad.q6bq8sm (Thaxter et al., 2019a) and R code via Zenodo: https://doi.org/10.5281/zenodo.3363888 (Thaxter et al., 2019b).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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