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Seabird–wind farm interactions during the breeding season vary within and between years: A case study of lesser black-backed gull *Larus fuscus* in the UK

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ABSTRACT

The marine environment is increasingly pressured from human activities, such as offshore renewable energy developments. Offshore wind farms may pose direct risks to seabirds at protected breeding sites. However, changes in food availability may influence foraging behaviour and habitat use during the breeding season or between years. Consequently, seabird–wind farm interactions, and risks posed to populations, may vary over longer time scales, but this has seldom been quantified. We used GPS-telemetry to study the movements of 25 lesser black-backed gulls from the Alde–Ore Special Protection Area (SPA), UK between 2010 and 2012, while birds were associated with their breeding colony. Variation in movements away from the colony, offshore, and in operational, consented and proposed Offshore Wind Farm Areas ("OWFAs") was investigated: (1) between years and (2) across the breeding season, addressing: (3) sex-specific, (4) individual and (5) diurnal/nocturnal differences. The extent of overlaps with OWFAs varied between years, being greatest in 2010 (7/10 birds showing connectivity; area overlap: 6.2 ± 7.1%; time budget overlap: 4.6 ± 6.2%) and least in 2012. Marine habitats close to the colony were used before breeding. Birds spent little time offshore as incubation commenced, but offshore usage again peaked during the early chick-rearing period, corresponding with use of OWFAs. Individuals differed in their seasonal interactions with OWFAs between years, and males used OWFAs significantly more than females later in the breeding season. This study demonstrates the importance of tracking animals over longer periods, without which impact assessments may incorrectly estimate the magnitude of risks posed to protected populations.

1. Introduction

The marine environment is under increasing pressure from human activities, such as fisheries, shipping and boat traffic, oil and gas, and renewable energy (Syvitski et al., 2005; Halpern et al., 2008). Offshore wind farms are a key part of the UK Government's plan to obtain 15% of energy from renewable sources by 2020 (DECC, 2009). It is therefore important to properly quantify the potential impacts that proposed offshore wind farms, alongside those operational or consented (hereafter together termed as Offshore Wind Farm Areas, "OWFAs"), could have on marine wildlife and habitats.

Seabirds are key components of marine ecosystems, and may be affected by offshore wind farms through direct collision mortality, displacement from foraging areas, diversion of flight paths, or through changes to habitats and prey (Garthe and Hüppop, 2004; Masden et al., 2009; Furness et al., 2013). In the UK, full consideration is given to each of these effects through the Environmental Impact Assessment (EIA) process. The potential impacts on populations of birds at protected sites, for example sites classified as Special Protection Areas (SPAs) under the European Union's Birds Directive (Directive 2009/147/EC), are given consideration through Habitats Regulations Assessments (HRA). Specific data on the links ("connectivity") between a particular SPA and the development of interest are often lacking, meaning that precautionary information, such as representative foraging ranges (Thaxter et al., 2012) may be required to evaluate potential impacts. Consequently, there is a pressing need to directly demonstrate connectivity between

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breeding sites (where breeding seabird species are classified as a SPA feature) and areas used at sea.

Greater availability and affordability of tracking technologies have offered an increasing number of ways to assess the likely impacts of offshore renewable energy developments on wildlife (Carstensen et al., 2006; Desholm et al., 2006; Scheidat et al., 2011). For seabirds, telemetry is a particularly useful tool in this regard (see Gyimesi et al., 2011; Langston et al., 2013; Bogdanova et al., 2014; Wade et al., 2014). Species-specific requirements and economic restrictions determine when and how many birds to tag and the types of tracking devices (hereafter "devices") used. Affordable short-life devices are very informative, but for seabirds their use is normally restricted to periods when devices can be deployed and retrieved from birds. Furthermore, information obtained for short periods may not be representative of a species' movements within the breeding season, or typical of movements in comparison to other years. It is well known that changes in food availability may alter the behaviour of birds through the course of a single breeding season and between years (Bearhop et al., 2001; Hamer et al., 2007; Pettex et al., 2012), which may lead to use of alternative foraging areas and different commuting patterns. Therefore, the movements of birds needs to be characterised over longer time periods (Bogdanova et al., 2014) to fully appreciate the potential for variation in seabird–wind farm interactions, and properly evaluate the risks posed to protected sites within EIAs.

For generalist species, some birds may exhibit dietary specialisation (Bolnick et al., 2003; Martins et al., 2008), resulting in individual differences in foraging behaviour. For instance among seabirds, different foraging tactics or particular trips may be required for certain prey (McCleery and Sibly, 1986; Watanuki, 1992; Woo et al., 2008). Foraging behaviour may also differ between sexes and therefore influence habitat use (Lewis et al., 2002; Thaxter et al., 2009). The relative probability of a flying bird colliding with an offshore wind turbine may also be greater at night than during the day due to reduced visibility (Garthe and Hüppop, 2004). However, differences in the movements of birds between daytime and night-time (Camphuysen, 2011), may also determine the risk of collision. Quantifying these additional sources of variability is necessary to build up a coherent picture of seabird–wind farm interactions.

This study focuses on the lesser black-backed gull, UK sub-species *Larus fuscus graellsii*, a breeding feature at 10 SPAs in the UK (Stroud et al., 2001). The foraging distribution and habitat associations of this species have been studied using at-sea surveys (e.g. Kubetzki and Garthe, 2003), and the species is increasingly being tracked from breeding colonies in Europe (Shamoun-Baranes et al., 2011; Klaassen et al., 2012). Lesser black-backed gulls may forage up to 180 km offshore during the breeding season (Thaxter et al., 2012). Hence, there is potential for birds from several UK colonies to forage in areas of OWFAs. Lesser black-backed gulls are considered at high collision risk (Furness et al., 2013), flying at heights (during commuting and foraging) within the rotor sweep zone (Johnston et al., 2014; Corman and Gathe, 2014), making it necessary to characterise their total area usage away from the breeding colony.

We used a long-term GPS system (Bouten et al., 2013) to investigate the movements of lesser black-backed gulls from an SPA in the UK. Using data collected over three separate years, we investigated whether time budgets, area utilisation, and in-turn the likelihood of interactions with OWFAs varied significantly: (1) between years, (2) during the breeding season, while also addressing potential (3) sex-specific, (4) individual, and (5) day-time and night-time variations in behaviour. There were very few constructed offshore wind farms at the time of the study to investigate any effects on behaviour before or after construction (4cOffshoreWind, 2015). Therefore our main aim was to assess potential exposure to OWFAs (proposed, operational and consented) and the sources of variation that can influence this.

2. Materials and methods

2.1. Study site and period

Lesser black-backed gulls were studied at a colony of 550–640 apparently occupied territories (AOTs) at Orford Ness (Marsh, 2013), part of the Alde–Ore Special Protection Area (SPA), Suffolk, UK (52°06′N, 1°35′E). The study took place from June 2010 to October 2012, from first recording of individuals at the colony to departure. This covered pre-breeding (return to colony to first egg, *ca.* February to May), breeding (incubation and chick-rearing, *ca.* May to July), and post-breeding periods (post-fledging or failed to departure, *ca.* July to October). The OWFAs within the potential foraging range of lesser black-backed gulls (Thaxter et al., 2012) at Orford Ness are given in Fig. 1 (see also Appendix A in Supplementary Information).

2.2. Capture methods and attachment of devices

Birds were caught at the nest site during early incubation using a walk-in wire mesh trap. During 2010, GPS devices (Bouten et al., 2013) were attached to 11 birds using either: a leg-loop harness ($n = 3$ birds), body harness with a breast strap ($n = 4$ birds), or wing harness ($n = 4$ birds). During 2011, devices were attached to a further 14 lesser black-backed gulls using a wing harness (Thaxter et al., 2014). Birds were sexed using head and bill length measurements (2010, n = seven males, three females; 2011, n = seven males, six females; two unidentified, one in each year, due to uncertainty) that were recorded along with body mass on capture (Coulson et al., 1983; Camphuysen, 2011). One GPS device deployed in 2010 provided no data (male bird), giving a total sample size of 24 birds across all years for further analysis. The total weight of devices (plus harness) was 21 g (<3% body mass, mean weight 851 ± 85 g, range: 710–955 g). The potential effects of the GPS devices and harnesses used in this study were assessed through comparison with a separate group of control birds. There were no significant differences between harness and control groups in measures of productivity or over-winter survival ($P > 0.05$), indicating that the GPS device and wing harness had negligible effects for the species in this study (C.B. Thaxter Unpublished data); thus behaviour is considered representative.

2.3. Productivity and breeding periods

The nests of tagged individuals were monitored during their breeding season of capture through approximately weekly visits in order to assess the variation in the productivity of the colony between years and the timing of breeding periods. Tall vegetation and mobility of chicks prevented the following of nest survival to fledging. For the same reasons, the nests of tagged birds could not be monitored beyond the first season in which they were tagged. Therefore, the productivity of additional ("control") nests of unmarked birds was monitored in 2011 ($n = 46$) and 2012 ($n = 51$). Productivity was assessed through: (i) number of eggs hatched per nest, and (ii) number of chicks present at the end of monitoring (up to mid-July). Where there was uncertainty (between colony visits), mean minimum and maximum estimates were calculated. Chicks were monitored up to 11 July in 2010, 9 July in 2011 and 23 May 2012; in 2012 subsequent visits in early June to July revealed the colony had suffered a breeding failure.

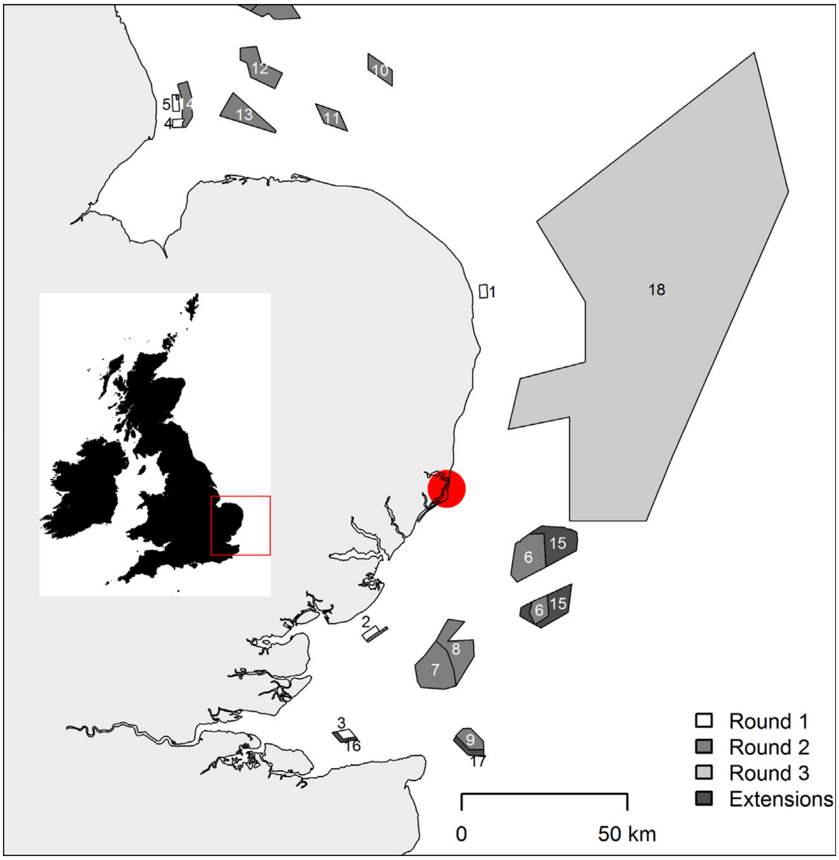

Fig. 1. Location of Orford Ness, Alde–Ore SPA, (red circle) in proximity to operational Round 1 and Round 2 offshore wind farms, proposed extensions and Round 3 offshore development zones at the time of the study. Round 1: 1 Scroby Sands, 2 Gunfleet sands, 3 Kentish Flats, 4 Lynn, 5 Inner Dowsing; Round 2: 6 Greater Gabbard, 7 London Array Phase 1, 8 London Array Phase 2, 9 Thanet, 10 Dudgeon, 11 Sherringham Shoal, 12 Race Bank, 13 Docking Shoal, 14 Lincs; Extensions: 15 Galloper, 16 Kentish Flats 2, 17 Thanet 2; Round 3: 18 East Anglia development zone. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Chicks were monitored on average between five (±9 SD) and 14 (±9 SD) days after hatching and up to a maximum of 26–35 days after hatching (the difference in values representing uncertainty in hatching dates).

2.4. Processing of data

2.4.1. Trip statistics

Time-stamped GPS data were downloaded remotely from devices to a field-based laptop (Bouten et al., 2013). A virtual perimeter of *ca.* 200 m^2 around the colony was used to identify when birds were ‘within’ the colony attending nest sites, or away from the colony on trips. Devices were set to record at 5–10 min intervals (depending on battery quality) while the birds were away from the colony and at 30 min intervals while they were at the colony, in order to help maintain battery life. To ensure that battery power was maintained outside the breeding season, the GPS devices were also set to 15–30 min intervals in mid-July before birds departed the colony, and hence sampled at a lower rate during the post-breeding, over-winter and pre-breeding periods. For all trips, we calculated (a) an offshore foraging range (the maximum distance reached offshore from the colony); (b) the total travel distance per trip (by summing distances between GPS points along the route); and (c) trip duration (time elapsed between departure and return).

2.4.2. Time budgets

For all trips, we calculated the total, diurnal and nocturnal (defined by the periods between local sunrise and sunset) time spent in offshore and inland areas and time spent in OWFAs (see Appendix A) within consecutive five-day periods. Together with time at the nest, this enabled calculation of the time spent: (a) away from the nest, (b) offshore, and (c) in OWFAs.

2.4.3. Area usage

The area utilisation of birds away from the colony was assessed using kernel density estimation (KDE, Worton, 1989). The 50%, 75% and 95% KDEs of the utilisation distribution, were taken to represent the core, middle, and total areas, respectively. Least Squares Cross Validation (LSCV) was used to estimate the smoothing parameter (e.g. Hamer et al., 2007; Thaxter et al., 2009), alongside additional visual examination of utilisation distributions and a range of bandwidths (Wade et al., 2014). Data were filtered to a 30 min rate for spatial analysis to circumvent unequal sampling rates throughout the pre-breeding, breeding and post-breeding periods (see above). For five-day periods through the season, for each individual we calculated the: (a) total area usage away from the nest, (b) area usage offshore, and (c) area usage within OWFAs. Area usage offshore and within OWFAs was calculated through simple assessment of percentage overlaps between KDEs and these respective areas. To allow comparison to total time spent away from the nest, further analyses focus on the total spatial area usage using the 95% KDE. Note, however, that the total 95% KDEs may also include areas at sea used less often by birds. Therefore, appropriate interpretation of OWFA overlaps is required to avoid potential exaggeration of impacts. Temporal and spatial overlaps with specific OWFAs are provided in Appendix A using both 50% and 95% KDEs.

2.5. Analysis

To assess annual and sex-specific variation in trip statistics, time budgets and area usage, General Additive Mixed-effects Models (GAMMs) were fitted using R library "mgcv" (Wood, 2006) with "year" (y) and sex (g) included as fixed effects and a smooth term of Julian date $s(d)$ with 8 degrees of freedom (d). An initial model (model 1) was constructed using the function gamm(mgcv) that was used to test for significance of main effects before interactions were included; response variables are given in Tables 1–3. A random effect for 'bird identity' (b) was included to account for pseudoreplication. To account for unequal sampling between individuals, models were weighted by the number of birds contributing data per five-day period, and a fixed effect of "number of GPS fixes" (F) was included for spatial analyses. An autoregressive (AR1) term was specified to account for temporal autocorrelation. Due to non-normal errors and the use of penalised quasi-likelihood (PQL), model selection was primarily conducted through backwards step-wise selection (see Appendix C for more details). A separate model was then constructed using function gam(mgcv) to examine differences in seasonal patterns between years and sexes, and individual differences between years (model 2, see below), by specifying the interactions $s(d,g)$, $s(d,y)$, and $r(b,y)$. Tests for smooth interaction terms are reported using change in deviance F-tests, but this was considered approximate. Therefore model selection was also carried out using Akaike's Information Criterion adjusted for small sample sizes (AICc). This provided verification of the significance of interaction terms (see Appendix C). Significant terms are presented from the best-fitting model after sequential removal of non-significant terms. Non-significant terms are presented prior to their subsequent removal. Where models were compositional (such as proportion of time spent offshore), quasi-binomial errors were used, with QAICc used in place of AICc (Bolker 2014), correcting for overdispersion ($\hat{c}$). All other models were fitted with negative binomial or Poisson error distributions, or in the case of trip statistics were better fitted through a log-transformed response. An example global model for the total 95% KDE area size (A), fitted with a negative binomial distribution, was given as:

$$\log(A_i) = \beta_0 + \beta_1 y_i + \beta_2 g_i + \beta_3 F_i + f_1(d_i, y_i) + f_2(d_i, g_i) + r_1(b_i, y_i) + \varepsilon$$

where i is the five-day period, f_j are smoothed functions, and r_j is the random effect, with interactions specified between y_i and g_i, respectively. Due to centering constraints parametric terms (g and y) were included in models containing interactions with Julian date. Individual variation within the season was examined separately with a single interaction of Julian date and bird ID $r(b,d)$ to avoid over-parameterisation of the fully saturated model. Equivalent models were fitted for day and night movements, and are presented in Appendices B and C. Means are presented ±1 SD, unless otherwise stated. All analyses were performed using R Version 2.15.0 (R Development Core Team, 2013).

3. Results

3.1. Breeding productivity

Based on estimated first egg hatching dates and maximum incubation and chick-rearing durations from the literature (Robinson, 2005), estimated incubation periods for the colony were: 7 May–17 June 2010 (Julian date, 127–168), 5 May–12 June 2011 (125–163), and 14 April–23 May 2012 (105–144), with chick-rearing estimated to be: 3 June–27 July 2010 (154–208), 1 June–22 July 2011 (152–203), and 11 May–2 July 2012 (132–184). Note that this approach expressed uncertainty in breeding periods and in turn an overlap in the end of incubation and start of chick-rearing. The mean number of eggs hatched per nest was between 0.5 ± 0.7 and 2.4 ± 0.9 in 2010, between 1.3 ± 1.1 and 2.2 ± 1.1 in 2011, and between 0.2 ± 0.6 and 2.6 ± 0.9 in 2012 (mean minimum and mean maximum estimates, pooled across tagged and control nests). During 2010 and 2012, no chicks survived past mid-July; nests failed either due to direct predation of eggs, chicks and adults, or colony disturbance from

Table 1

Summary of significant parametric and smoothed terms and beta (ß)-coefficients from GAMM temporal analyses of trip duration, offshore foraging range, and distance travelled per trip, investigating effects of sex (g), year (y), Julian date $s(d)$ and bird ID (b), and their subsequent interactions. ß-coefficients for sex are for female and male (1 and 2), and for year are 2010, 2011, 2012 (1–3); equivalent AIC tables from model selection using GAMs are shown in Appendix C. Also shown are values of deviance explained ("Dev") from global models, and an asterisk (∗) indicates significant ($P < 0.05$) coefficients or smooth terms (effective degrees of freedom = "edf"). Model 1 (M1) specified main effects prior to interactions being included (M2).

Main effects	*M*	Var	df	*F*	*P*	ß-coefficients/edf		
						1	2	3
(i) Trip duration	1	g	1	32.01	<0.001	1.43 ± 0.08*	−0.35 ± 0.06*	
Dev = 8.42%; scale 10.20		y	2	31.90	<0.001	1.43 ± 0.08*	−0.22 ± 0.08*	−0.03 ± 0.08
		$s(d)$	5.52	63.54	<0.001			
Dev = 15.32%; scale 9.47	2	$s(d,g)$	5.21	30.54	<0.001	5.24*	5.22*	
		$s(d,y)$	5.41	8.85	<0.001	1.00*	3.38*	5.13*
		(b,y)	13.34	32.85	<0.001	3.16*	13.31*	12.64*
		b	15.37	21.43	<0.001	15.41*		
(ii) Offshore foraging range	1	g	1	0.01	0.950	4.38 ± 0.47*	−0.02 ± 0.28	
Dev = 42.34%; scale 6.78		y	2	5.21	0.006	4.26 ± 0.32*	−0.08 ± 0.34	−0.42 ± 0.37
		$s(d)$	6.30	36.13	<0.001			
Dev = 47.28%; scale 6.28	2	$s(d,g)$	5.01	5.65	<0.001	5.87*	5.06*	
		$s(d,y)$	4.18	5.26	<0.001	1.04*	4.59*	4.10*
		(b,y)	3.46	14.25	<0.001	0.001	11.35*	5.87*
		b	11.25	8.91	<0.001	11.18*		
(iii) Distance travelled	1	g	1	0.81	0.369	3.34 ± 0.16*	−0.02 ± 0.28	
Dev = 9.98%; scale 19.51		y	2	8.39	<0.001	3.22 ± 0.03*	0.02 ± 0.12	−0.17 ± 0.13
		$s(d)$	6.44	48.92	<0.001			
Dev = 12.51%; scale 19.00	2	$s(d,g)$	5.08	4.96	<0.001	5.00*	5.98*	
		$s(d,y)$	4.29	7.61	<0.001	1.00*	5.28*	3.86*
		(b,y)	13.29	12.04	<0.001	3.39*	13.10*	11.38*
		b	14.79	14.11	<0.001	14.59*		

Table 2
Summary of significant parametric and smoothed terms and beta (ß)-coefficients from GAMM temporal analyses of time away from the nest, time spent offshore, and time spent in OWFAs, investigating effects of sex (g), year (y), Julian date $s(d)$ and bird ID (b), and their subsequent interactions. See Table 1 for further description.

Main effects	*M*	Var	df	*F*	*P*	ß-coefficients/edf		
						1	2	3
(i) Time away from nest	1	g	1	0.001	0.979	1.32 ± 0.30*	−0.01 ± 0.34	
Dev = 62.95%; scale 1.37		y	2	64.16	<0.001	1.31 ± 0.21*	−0.72 ± 0.15*	−0.13 ± 0.15
		$s(d)$	5.21	46.22	<0.001			
Dev = 80.07%; scale 0.76	2	$s(d,g)$	5.84	7.57	<0.001	5.25*	6.54*	
		$s(d,y)$	6.69	34.87	<0.001	1.29*	5.32*	7.11*
		(b,y)	16.52	20.82	<0.001	7.74*	16.61*	12.65*
		b	22.32	24.12	<0.001	21.26*		
(ii) Time spent offshore	1	g	1	0.33	0.566	−1.76 ± 0.42*	−0.21 ± 0.36	
Dev = 50.47%; scale 1.10		y	2	51.53	<0.001	−1.97 ± 0.34*	−1.72 ± 0.23*	−2.72 ± 0.26*
		$s(d)$	6.33	27.58	<0.001			
Dev = 64.61; scale 0.82	2	$s(d,g)$	1.41	22.87	<0.001	4.18*	6.49*	
		$s(d,y)$	3.05	6.05	<0.001	5.04*	6.43*	7.09*
		(b,y)	18.00	12.50	<0.001	7.96*	15.63*	11.45*
		b	21.80	17.39	<0.001	20.78*		
(iii) Time spent in OWFAs	1	g	1	2.59	0.108	−7.51 ± 1.03*	1.22 ± 0.76	
Dev = 68.09%; scale 0.24		y	2	39.98	<0.001	−6.89 ± 0.88*	−1.50 ± 0.22*	−2.97 ± 0.34*
		$s(d)$	4.08	20.87	<0.001			
Dev = 73.65%; scale 0.20	2	$s(d,g)$	2.15	2.83	0.056	3.98*	3.42*	
		$s(d,y)$	5.36	15.18	<0.001	3.24*	3.71*	4.25*
		(b,y)	11.71	5.58	<0.001	7.94*	15.14*	8.94*
		b	21.78	39.77	<0.001	20.48*		

Table 3
Summary of significant parametric and smoothed terms and beta (ß)-coefficients from GAMM spatial analyses of total area usage, offshore overlap, and overlap with OWFAs, investigating effects of sex (g), year (y), Julian date $s(d)$, number of fixes (F) and bird ID (b), and their subsequent interactions. See Table 1 for further description.

Main effects	*M*	Var	df	*F*	*P*	ß-coefficients/edf		
						1	2	3
(i) Total area usage	1	g	1	0.16	0.691	−0.31 ± 0.20	0.08 ± 0.19	
Dev = 51.05%; scale 2.93		y	2	14.39	<0.001	−0.42 ± 0.17*	−0.24 ± 0.15	−0.69 ± 0.17*
		$s(d)$	5.70	14.38	<0.001			
		F	1	19.56	<0.001	0.003 ± 0.001*		
Dev = 61.31%; scale 2.38	2	$s(d,g)$	5.45	9.97	<0.001	5.43*	6.27*	
		$s(d,y)$	7.52	1.73	0.094	3.19*	5.50*	5.41*
		(b,y)	12.44	7.93	<0.001	7.50*	16.00*	9.56*
		b	22.40	18.32	<0.001	20.67*		
(ii) Offshore overlap	1	g	1	0.47	0.494	−0.16 ± 0.28	0.14 ± 0.20	
Dev = 44.23%; scale 1.30		y	2	9.97	<0.001	−0.15 ± 0.21	−0.59 ± 0.21*	−1.02 ± 0.24*
		$s(d)$	4.97	21.23	<0.001			
		F	1	0.52	0.472	−0.001 ± 0.001		
Dev = 57.16%; scale 1.02	2	$s(d,g)$	0.36	103.90	<0.001	4.03*	7.25*	
		$s(d,y)$	3.24	2.50	0.054	3.57*	5.37*	4.98*
		(b,y)	14.79	11.54	<0.001	7.74*	16.05*	10.55*
		b	20.96	12.05	<0.001	17.23*		
(iii) Overlap with OWFAs	1	g	1	2.36	0.125	−6.79 ± 0.92*	1.09 ± 0.71	
Dev = 67.87%; scale 0.45		y	2	23.25	<0.001	−6.18 ± 0.78*	−1.27 ± 0.29*	−2.61 ± 0.39*
		$s(d)$	3.91	16.35	<0.001			
		F	1	9.23	0.002	0.007 ± 0.002*		
Dev = 73.64%; scale 0.39	2	$s(d,g)$	1.67	8.64	0.001	4.07*	3.28*	
		$s(d,y)$	4.96	17.11	<0.001	2.95*	4.03*	5.28*
		(b,y)	12.66	5.86	<0.001	7.84*	15.67*	9.76*
		b	19.18	35.86	<0.001	17.89*		

flooding. In 2011, the mean number of chicks raised per nest up to 9 July was between 0.7 ± 0.9 and 2.0 ± 0.8.

3.2. Annual variation in habitat usage

There was a significant difference between years in all trip statistics (Table 1). Trips were longer in duration, covered more distance and reached further offshore in 2010 than other years (Tables 1 and 4). During 2010, more time was spent away from the nest offshore and in OWFAs (Table 2) than in 2011 and 2012. The use of OWFAs was significantly greater in 2010 than other years (Tables 2 and 3, Fig. 2). The proportion of birds showing connectivity with OWFAs was similar between 2010 (7/10 birds) and 2011 (14/18 birds), but slightly lower in 2012 (8/14 birds). All birds used the large Round 3 East Anglia development zone, but due to their smaller sizes, other operational, consented and proposed offshore wind farms made up a much smaller proportion of overlaps (see Appendix A).

3.3. Seasonal variation in habitat usage

Best fit models all included Julian date, and some were improved through an interaction of year ∗ Julian date (Tables 1–3, Appendices B and C). Trips decreased significantly in duration, range and

Table 4
Means and range across all consecutive five-day periods per year for measures of trips statistics, time budgets, and area usage for (a) years, 2010, 2011 and 2012 and (b) males and females; specific wind farm zones overlapped during the study are given in Appendix A.

	Measure	2010 (10 birds)			2011 (18 birds)			2012 (14 birds)		
		Mean ± SD	Range	*N*	Mean ± SD	Range	*N*	Mean ± SD	Range	*N*
(a)										
Trip statistics	Trip duration (h)	8.6 ± 3.7	<0.1–166.7	10	4.8 ± 1.6	0.1–216.4	18	6.5 ± 2.7	<0.1–253.9	14
	Offshore foraging range (km)	33.5 ± 16.1	0.4–158.7	10	25.1 ± 10.9	0.8–124.0	18	14.7 ± 5.7	0.4–158.5	14
	Distance travelled (km)	41.7 ± 35.4	0.3–893.7	10	34.2 ± 16.6	<0.1–998.7	18	22.3 ± 8.0	<0.1–943.1	14
Time budgets	Time away from nest (%)	78.3 ± 17.6	17.2–100	10	60.4 ± 15.9	11.3–100	18	71.5 ± 12.6	12.5–100	14
	Time spent offshore (%)	14.1 ± 15.3	0–94.4	10	6.2 ± 7.0	0–68.3	18	7.7 ± 4.9	0–100	14
	Time spent in OWFAs (%)	4.6 ± 6.2	0–52.0	7	1.2 ± 2.0	0–24.9	14	0.2 ± 0.3	0–10.3	8
Area usage	Total area usage – size of 95% KDE (km^2)	1 069 ± 904	211–6 077	10	916 ± 498	135–4 477	18	592 ± 195	33–2 869	14
	Offshore overlap (%)	44.2 ± 15.7	0–92.0	10	34.0 ± 10.6	0–93.0	18	32.9 ± 8.9	0–76.1	14
	Overlap with OWFAs (%)	6.2 ± 7.1	0–61.9	7	3.2 ± 4.3	0–44.2	11	0.6 ± 1.0	0–32.6	4

	Measure	Females (*n* = 9 birds)			Males (*n* = 13 birds)		
		Mean ± SD	Range	*N*	Mean ± SD	Range	*N*
(b)							
Trip statistics	Trip duration (h)	7.5 ± 1.9	0.1–231.3	9	5.4 ± 2.0	<0.1–253.9	13
	Offshore foraging range (km)	20.5 ± 6.9	0.5–158.7	9	25.2 ± 8.6	0.4–124.0	13
	Distance travelled (km)	31.0 ± 8.4	<0.1–943.1	9	29.7 ± 13.7	<0.1–998.7	13
Time budgets	Time away from nest (%)	71.1 ± 9.9	11.3–100	9	67.3 ± 19.9	12.5–100	13
	Time spent offshore (%)	5.9 ± 4.8	0–100	9	10.2 ± 11.2	0–94.0	13
	Time spent in OWFAs (%)	0.5 ± 0.8	0–41.5	6	2.6 ± 4.9	0–52.0	11
Area usage	Total area usage – size of 95% KDE (km^2)	750 ± 274	129–6 077	9	821 ± 370	33–4 055	13
	Offshore overlap (%)	32.8 ± 7.2	0–92.2	9	38.0 ± 15.0	0–93.0	13
	Overlap with OWFAs (%)	1.2 ± 1.7	0–49.0	6	4.3 ± 5.3	0–61.9	11

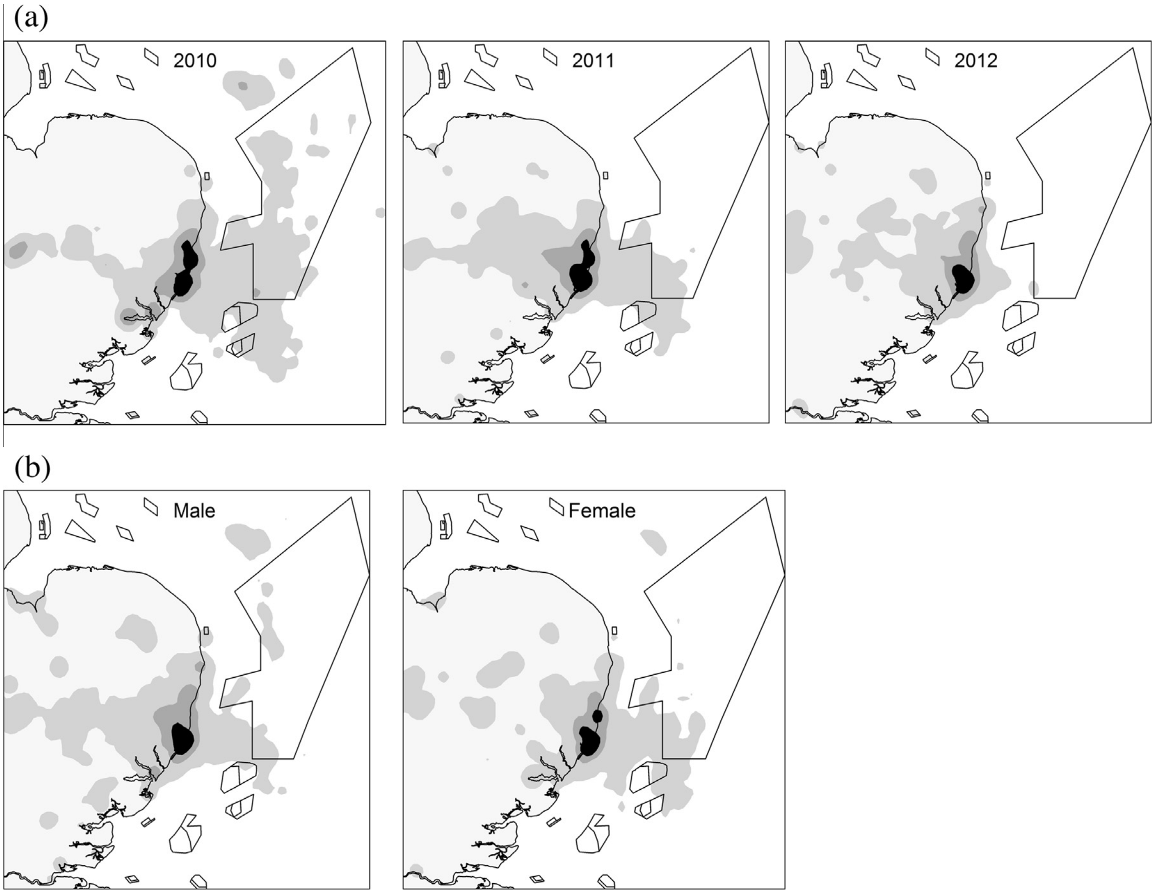

Fig. 2. Spatial area usage by lesser black-backed gulls given by: (a) year and (b) sex. Shown are the 95% KDE (light grey) representing total area usage, 75% KDE (medium grey) and 50% KDE (black), representing core area usage.

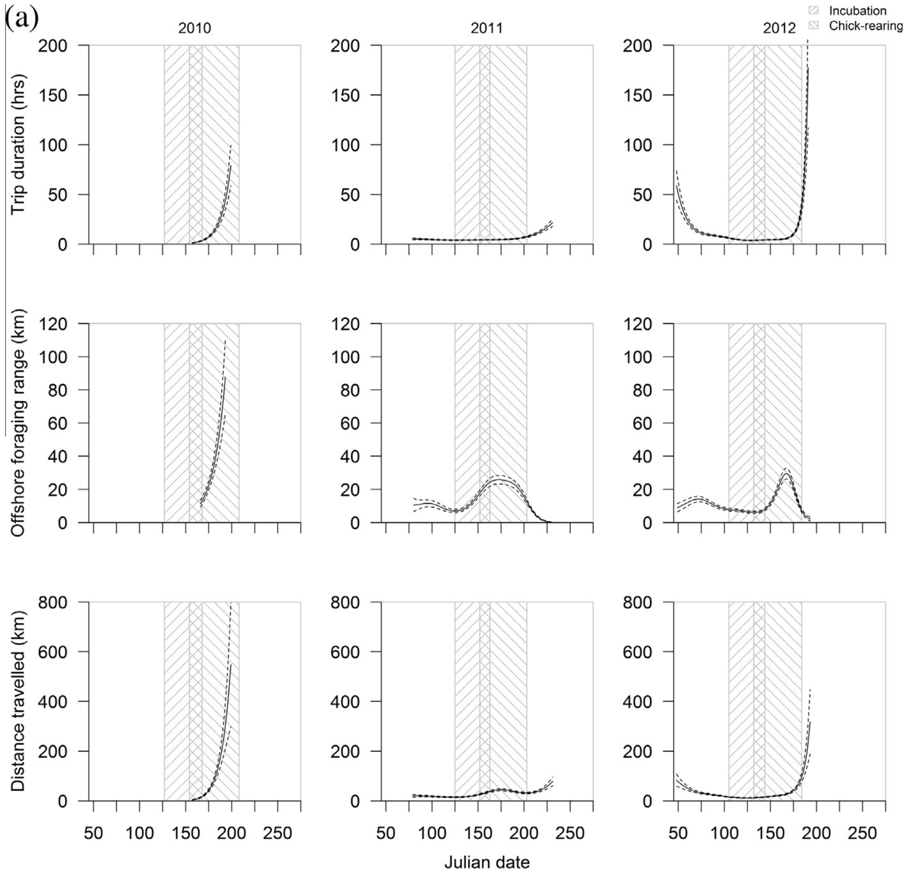

Fig. 3. Annual differences in seasonal relationships of: (a) summary statistics, (b) time budgets and (c) spatial area usage. Each graph is a modelled GAMM output (±SE); the significance of the effect is given in Tables 1–3 and Appendix C.

distance travelled throughout pre-breeding until the start of incubation (Fig. 3a), thereafter trips gradually increased. Offshore foraging range peaked during the late chick-rearing period (Fig. 3a), however significant year ∗ Julian date parameters indicated annual variation in these seasonal patterns (Table 1, Fig. 3a). In particular, during 2011, trip durations and distances travelled increased more slowly with Julian date than in other years, where sharp increases were recorded late in the season. At the end of the season, apparent trip durations increased as birds were no longer constrained to the colony but, in some instances, still remained in the surrounding area (Fig. 3a and b).

Birds spent significantly less time offshore from pre-breeding to incubation (Table 2, Fig. 3b), but spent significantly more time offshore during the early chick-rearing period (modelled peak 20 June, 11.2 ± 2.2[SE]%). This peak was significantly earlier (Table 2, Appendix C) in 2011 (Fig. 3b; 16 June, 7.0 ± 1.9[SE]% time budgets), greatest and latest in 2010 (28 June, 36.2 ± 7.8[SE]%) and smallest in 2012 (20 June, 2.8 ± 0.9[SE]%). Consequently, birds used OWFAs significantly more during the early chick-rearing period, and most of all in 2010 (peaks: 27 June 2010, 5.7 ± 2.7[SE]%; 21 June 2011, 0.9 ± 0.5[SE]%; 19 June 2012, 0.4 ± 0.2[SE]%, Fig. 3b, Table 2, Appendix C). During pre-breeding, birds spent longer offshore overnight (Fig. 3b) close to the colony (Fig. 3a); hence OWFAs were not used at this stage in the season.

Total area usage (95% KDE) decreased significantly during pre-breeding in 2011 and 2012, coinciding with the start of incubation, but peaked again later during breeding (Fig. 3c). A range contraction was recorded post-breeding thereafter increasing slightly again prior to the over-winter period. This pattern was not significantly different between years (Table 3, Fig. 3c, Appendix C). Likewise, the percentage overlap with offshore areas was similar in pattern and magnitude between years (Table 3, Fig. 3c, Appendix C), albeit highest in 2010 (Fig. 3c; 25 June, 59.4 ± 4.7[SE]%). However, patterns of spatial overlaps with OWFAs were significantly different between years peaking during early chick-rearing, with the largest and latest peaks recorded in 2010 (28 June 2010, 16.3 ± 7.5[SE]%; 16 June 2011, 4.6 ± 2.2[SE]% 16 June 2012 2.5 ± 1.3[SE]%).

3.4. Sex-specific habitat usage

After accounting for other main effects, there were no overall sex-specific differences in any trip statistic (Tables 1–3), with the exception of trip duration, which was significantly longer for females than males (Table 1). However, males and females differed significantly in the seasonal timing of peaks and troughs in relationships across Julian date (Tables 1–3, Appendix C). For example, trip durations, offshore foraging ranges and distances travelled per trip decreased from pre-breeding to the start of incubation and thereafter increased, however, males showed a significantly earlier pre-breeding decrease in these patterns than females (Fig. 4a, Table 1, Appendix C).

The time spent away from the nest also varied significantly between sexes across the season (Tables 1–3, Appendix C); the time away from the nest reduced to a minimum proportion that was significantly smaller and earlier for males than for females (Fig. 4b, lowest modelled proportion: male, 42.6 ± 7.1[SE]% of time budgets, 14 May; female, 52.9 ± 8.3[SE]% of time budgets, 01 June).

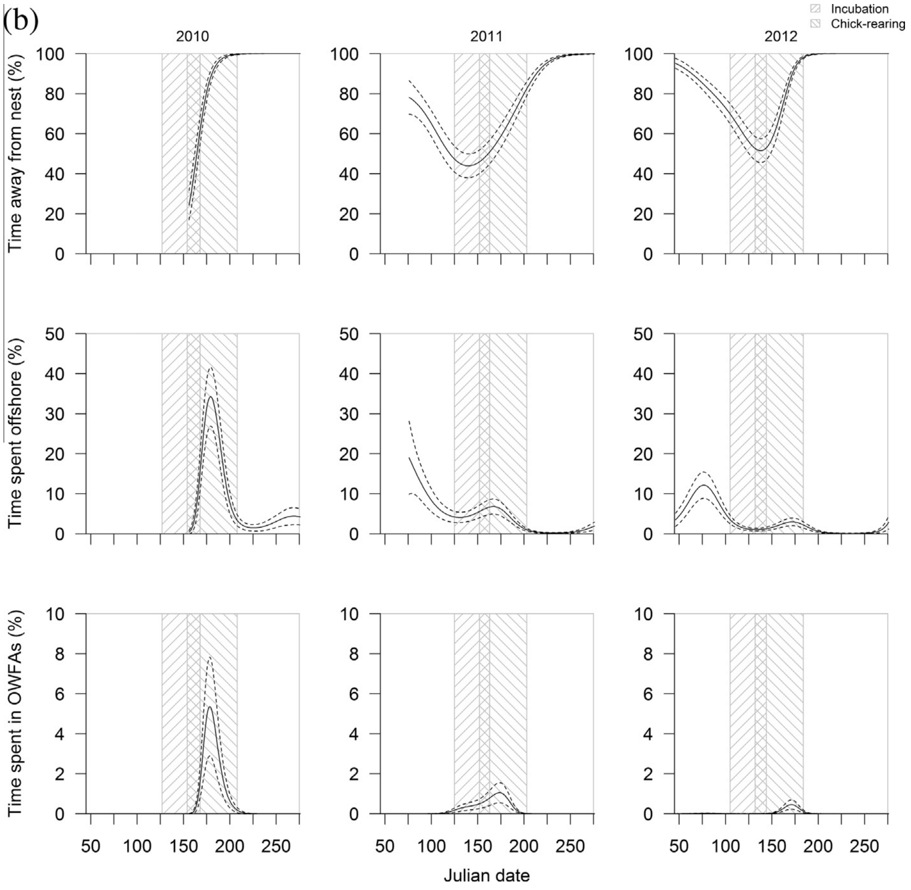

Fig. 3 (*continued*)

Males also spent significantly more time than females offshore at particular times of the season, the peaks being earlier and larger during chick-rearing for males (19 June, 15.6 ± 3.6[SE]%) than for females (25 June, 5.6 ± 1.8[SE]%; Fig. 4b).

Total area usage also varied significantly across Julian Date by sex (Table 1), peaking later in the breeding season for females (Fig. 4c). The extent of offshore usage differed between sexes, with males showing a larger peak in the proportional 95% KDE overlap with offshore areas (52.6 ± 3.9[SE]%) during early chick-rearing than females (37.8 ± 4.3[SE]%), which resulted in a significant difference between sexes in the extent of overlap with OWFAs at this time (males: 6.8 ± 3.4[SE]% on 18 June; females: 1.5 ± 1.0[SE]% on 22 June; Fig. 4c).

3.5. Individual variation in behaviour

The random bird ID term was highly significant in nearly every analysis of trip statistics and consequently in the extent of offshore area usage and OWFA interactions (Tables 1–3, Appendix C, $P < 0.001$), indicating significant individual differences. There were some similarities between individuals in the timing of peaks throughout the season in overlaps with offshore areas and OWFAs (see Appendix D). However, birds differed significantly in area usage during the course of a season (bird ID $*$ Julian Date, ΔAICc $\leqslant 2.0$ in all cases). Likewise, individuals did not always exhibit the same patterns between years (bird ID $*$ Year, Tables 1–3, Appendix C). For instance, one individual foraged offshore during 2010 (tracked from mid-June to early July) but foraged more inland in the following two years when more complete seasonal data were available (late-March to early-July). In contrast, another bird foraged solely inland, with very similar patterns seen between 2011 and 2012 (Appendix D).

4. Discussion

4.1. Annual variation in habitat use

The majority of lesser black-backed gulls in this study showed connectivity with OWFAs in the area in each year of the study. The Round 3 East Anglia development zone was used most of all, partly because it was larger than other OWFAs (Fig. 1). However, only parts of the East Anglia zone presently contain proposed projects (4cOffshoreWind, 2015), therefore reducing the likelihood that birds using this area would actually interact with turbines. Despite the number of birds showing connectivity, this translated into relatively small spatio-temporal overlaps (Tables 2 and 3, Appendix A). A similar finding was made by Camphyusen (2011) for two existing offshore wind farms in the Netherlands. We also found that the extent of connectivity and overlaps with OWFAs varied considerably between years, being greatest in 2010. By contrast, only moderate annual variability in at-sea distributions of lesser black-backed gulls has been reported elsewhere (Schwemmer and Garthe, 2008). During the breeding season, lesser black-backed gulls take a range of terrestrial and marine prey, including small fish and invertebrates, as well as refuse and discards (Kubetzki and Garthe, 2003; Camphuysen, 1995; Bustnes et al., 2010). Conceivably, alterations to foraging habitat or distribution of these prey types between years may have played a part in annual patterns in this study as has been reported for other seabirds (e.g. Hamer et al., 2007; Pettex et al., 2012). Foraging

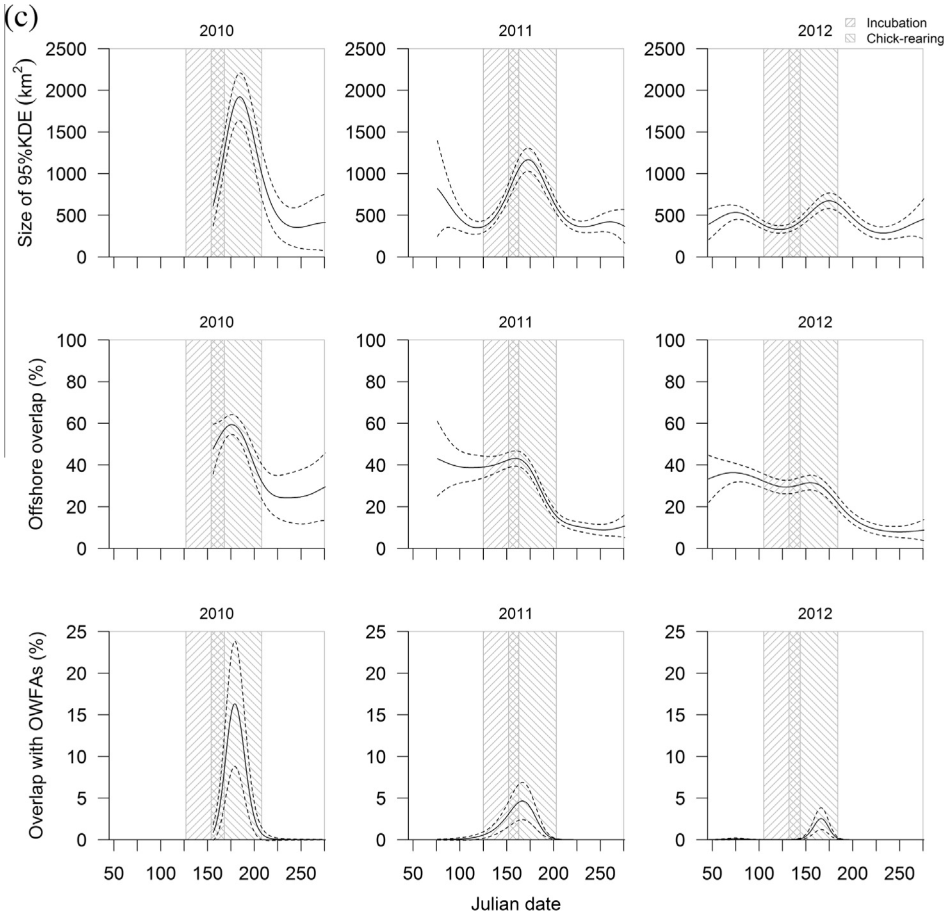

Fig. 3 (*continued*)

behaviour may also change in response to alterations to fisheries activity (Torres et al., 2011), or dietary switching to anthropogenically-sourced resources (Ramírez et al., 2012). Indeed, the types of fishing practice and effort in the study area vary annually in both distribution and extent (Jennings et al., 2012), which could have then influenced the extent of offshore habitat usage by lesser black-backed gulls.

4.2. Seasonal habitat use

The use of offshore areas by lesser black-backed gulls peaked during pre-breeding as birds spent a relatively large proportion of their time offshore close to the colony (see Appendix D). This matched similar patterns previously observed at Texel, Netherlands (Shamoun-Baranes et al., 2011). Offshore habitat use then reduced towards the start of incubation, but a second peak occurred during the early chick-rearing period, corresponding to an increase in the use of OWFAs at this time. Thereafter, birds increasingly used inland areas during the post-breeding period, prior to over-winter departure. This overall seasonal pattern may reflect the stage of the breeding season and, in particular, the onset of chick-rearing and nest failure.

When productivity of the colony was greatest in 2011, birds gradually spent more time offshore and in OWFAs and made trips that were further offshore as the chick-period progressed (Fig. 2a–c). This pattern may represent changes in habitat selection or prey switching to meet needs of the chicks. Habitat use and dietary changes across the season have been recorded for many gull species. For instance, Schwemmer and Garthe (2008) recorded black-headed gulls *Chroicocephalus ridibundus* switching from inland to marine feeding sites, attributed to a decrease in prey availability/quality in terrestrial habitats. Other studies have suggested dietary switching in gulls accommodates the nutritional needs of newly hatched chicks and their ability to physically manipulate and swallow particular foodstuffs (e.g. Kirkham and Morris, 1979; Annett and Pierotti, 1989; Nogales et al., 1995).

If food supplies are scarce in a given year, productivity can be affected by a reduced feeding rate, leading to chick starvation and predation, often by other gulls nesting at the same breeding colony (Bukacinski et al., 1998). Although productivity differences are not always reflected in foraging behaviour (Kim and Monaghan, 2006), demographics can influence diet and habitat use (Washburn et al., 2013). For example, the observed changes in habitat use and behaviour may be linked to failed breeders that no longer have constraints on the use of particular habitats and prey for their chicks. During 2010 and 2012, the increases in trip duration of lesser black-backed gulls after 23 June (Julian date 175, see Fig. 3a), are almost certainly due to individual nest failures. However, the similarly low productivity and timing of failure for the colony in these years does not fully explain the annual differences in offshore usage between these two years.

Seasonal patterns in habitat use were not the same between years. Peaks in offshore usage were most pronounced in 2010 and lowest in 2012. Seasonal and inter-annual changes in oceanographic conditions can directly influence prey availability for seabirds through trophic linkages (Ito et al., 2009). Coupled with potential seasonal differences in the extent of fishery activity (Jennings et al., 2012), these factors could have influenced the

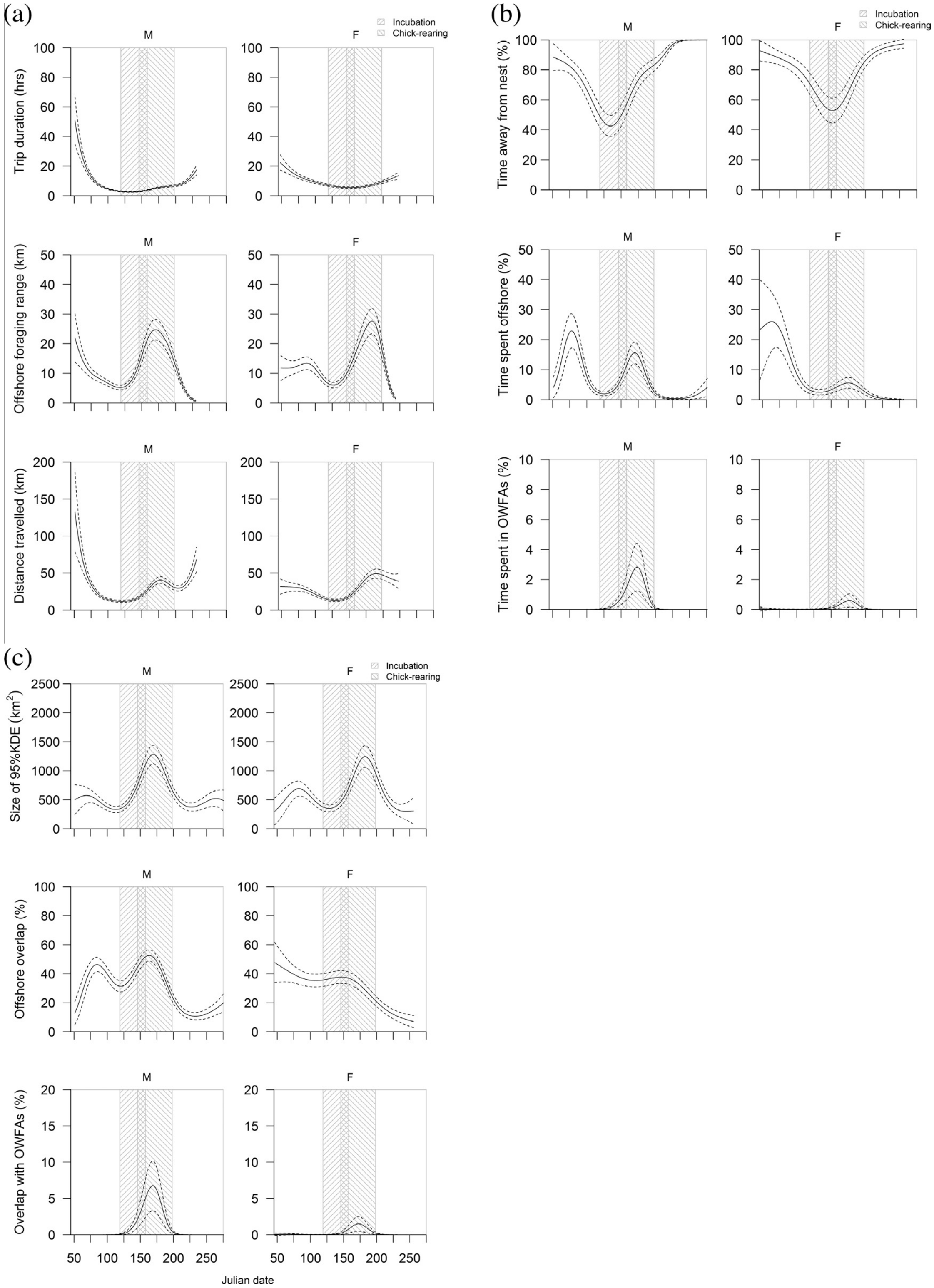

Fig. 4. Male (M) and female (F) differences in seasonal relationships of: (a) summary statistics, (b) time budgets and (c) spatial area usage. Each graph is a modelled GAMM output (±SE); the significance of the effect is given in Tables 1–3 and Appendix C.

inter-annual and seasonal patterns observed. Seasonal patterns were also different between males and females, and among other seabirds, sex-specific behaviours are frequently recorded (e.g. Greig et al., 1985; Lewis et al., 2002; Thaxter et al., 2009). At a separate colony of lesser black-backed gulls at Texel, Netherlands, males spent twice as long as females foraging in areas within or surrounding OWFAs than females who used a greater mosaic of different habitats (Camphuysen, 2011). Correspondingly, in the current study males had a greater spatial and temporal extent of offshore usage during chick-rearing than females, which translated into a significantly greater use of OWFAs at this time.

The second period of offshore habitat use and overlap with OWFAs occurred at an important stage of the breeding season, during the chick-rearing period. Offshore wind farms have the potential to affect the population through direct mortality such as collision, for which lesser black-backed gulls are vulnerable (Furness et al., 2013). Alternatively, displacement, barrier effects or changes to their prey may alter the time-energy budgets of foraging adults, reducing their body condition and the ability to provision and care for offspring. Consequently, adult survival, productivity and population dynamics could be affected. Although interactions with constructed wind farms in this study were small (Appendix A), this study has demonstrated a wider potential for increased exposure of lesser black-backed gulls to effects of offshore wind farms during the chick-rearing period.

4.3. Individual variation in behaviour

Individual birds varied significantly in their use of inland and offshore habitats, leading to differences in usage of OWFAs within breeding seasons and between years. For some individuals, seasonal patterns were similar, but the magnitude of the peaks was different between years; this also suggested the patterns were not simply an artefact of different groups of individuals tracked each year. Although we had no indication of diet in this study, individual foraging patterns may be linked to dietary specialisation, which for generalist predators like gulls, is widespread (Martins et al., 2008). Among seabirds, dietary specialisation (e.g. McCleery and Sibly, 1986; Watanuki, 1992) may result in particular foraging behaviours (Woo et al., 2008). The repeated use of offshore habitat by some, but not all, lesser black-backed gulls – possibly through a greater dependency on marine prey – increased their probability of interaction with OWFAs. An increased interaction with constructed wind farms through greater dependency on offshore habitats might be associated with an increased risk of collision mortality, or displacement or barrier effects and thus impacts on breeding productivity.

4.4. The importance of longer-term tracking

Assessments of home range are sometimes conducted for a limited number of years, using short-term devices for short periods during breeding (Thaxter et al., 2009; Soanes et al., 2012). Such data may then contribute to identifying potential marine protected areas (Le Corre et al., 2012), and assessing seabird–wind farm interactions (Soanes et al., 2012; Langston et al., 2013). Recent long-term research on European Shags *Phalacrocorax aristotelis* has shown that over a 15-year period, data from one year captured on average 54% of the foraging distribution, whereas eight years' data would be needed to reach 90% (Bogdanova et al., 2014). Our results also suggest that a long-term focus is ideally needed to assess the full extent of temporal and spatial variation in behaviour. Without such longer-term studies, seabird–wind farm interactions may not be suitably appraised within impact assessments.

In addition to quantifying variability, the number of birds tracked and the duration they are tracked for are important aspects. For example, tracking fewer individuals across the whole breeding season could negate the need for multiple years of data on a limited number of individuals tracked for a limited period during the breeding season (Girard et al., 2002; Soanes et al., 2013; Bogdanova et al., 2014). Such decisions may depend on the goals of the study. For instance, for characterisation of general area usage, fewer years of study may be acceptable. By contrast, monthly assessment of collision risk within impact assessments would benefit from a more detailed understanding of seasonal interactions with OWFAs across multiple breeding seasons. The latter would enable the impacts to be more accurately apportioned to protected sites. Further assessment of flight heights has also been conducted from boat-based (Johnston et al., 2014) and GPS tracking data (Corman and Gathe, 2014). This three-dimensional picture of habitat use will greatly improve our understanding of risks posed by OWFAs in particular areas at certain times of year.

4.5. Conclusions

With numerous anthropogenic pressures facing the marine environment, it is increasingly important to quantify the risks that renewable energy developments, such as offshore wind farms, may have on protected seabird populations. Precautionary information such as seabird foraging ranges is valuable in suggesting likely protected sites that may be affected (Thaxter et al., 2012). However, impact assessments are best served by direct data to assess connectivity, for which tracking information is playing an ever more central role. As the current study has shown, behaviour can be highly variable within seasons and between years, as well as between individuals and sexes. Emphasis should therefore be placed on gathering enough information on spatial and temporal variability in movements of seabirds alongside assessments of required sample sizes to meet the goals of the study.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.biocon.2015.03.027.

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