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Sexually distinct foraging strategies in an omnivorous seabird

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Abstract Intra-specific differences in foraging behaviour can have fitness consequences, especially during breeding. We combined GPS tracking data from 34 lesser black-backed gulls (*Larus fuscus*) encompassing 2029 foraging trips with dietary information and morphometric measurements to test the effect of breeding status and sex as well as body size on foraging behaviour. We found sexually distinct foraging strategies in this generalist seabird, which were maintained throughout the breeding season. The larger males travelled further from the colony than females, spent more time offshore, and remained longer at the nest during nest bouts. Males fed mostly on fisheries discards at offshore trawlers with few alternative resources nearby. Females foraged predominantly on land or nearshore and in the Wadden Sea, where they had multiple foraging options. Individuals differed in foraging behaviour along a continuum of predominantly terrestrial to predominantly marine foragers. Foraging range, trip duration, and the proportion of time at sea increased with wing length. Our findings did not support the usual inference that sexual segregation is mediated primarily by differences in competitive strength

as both sexes foraged substantially in competitive settings around fishing vessels, but in different habitats. Females accessed a wider variety of resources and a broad prey spectrum, by exploring a whole suite of foraging opportunities and habitats nearer the colony. Different behavioural strategies (a combination of individual specialisation and sexual segregation) during breeding could reduce intra-specific resource competition, competition between the sexes (and hence within a pair), or alternatively, reduce the risk of unbalanced food provisioning.

Introduction

An important aspect of foraging ecology is the extent to which individuals within a population exploit food resources in a different manner (Bolnick et al. 2003). Individual specialisation in foraging behaviour can influence intra-specific competition, individual fitness, population dynamics, and over longer time scales the evolution of species traits. Levels of individual specialisation vary among and within species and populations, reflecting a range of behavioural, physiological, and ecological mechanisms that generate such variation (Bolnick et al. 2003; Phillips et al. 2004; Bearhop et al. 2006; Lewis et al. 2006).

Most seabirds have bi-parental care, and provisioning of food is a major component of parental investment for both partners (Cramp and Simmons 1983). Parental investments do not need to be equal between males and females (Bennett and Owens 2002). Differences in parental care could be due to social dominance and competitive exclusion, niche specialisation or different reproductive roles, and these mechanisms might not be mutually exclusive (González-Solís et al. 2000; Phillips et al. 2004; Székely et al. 2007). Differences in foraging behaviour between

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sexes in sexually dimorphic species have often been attributed to body structure, affecting foraging efficiency or competitive ability (Conradt et al. 1999; González-Solís et al. 2000; Phillips et al. 2004). Smith (1966) found that the morphometric difference between the sexes was greatest for species that were allopatric with closely similar species. In the absence of inter-specific competition, selection was expected to favour divergence in adaptive features such as bill shape as a means to reduce intra-specific competition (Smith 1966).

The lesser black-backed gull, *Larus fuscus*, is a seabird that has recently colonised large parts of Europe and markedly increased in numbers over the past decades (Hagemeijer and Blair 1997). It is an omnivorous (generalist) seabird. They compete for prey in mixed flocks with other gulls and conspecifics, in association with fishing vessels or in natural feeding flocks at sea, and in cities, on meadows, and in agricultural fields on land (Cramp and Simmons 1983; Götmark 1984; Camphuysen 1995; Garthe and Hüppop 1998; Flore 1999; Schwemmer and Garthe 2005; Camphuysen et al. 2010). Lesser black-backed gulls are sexually dimorphic, but with a considerable overlap in size, where adult males are on average slightly larger than females (Coulson et al. 1983). Male lesser black-backed gulls have proportionally longer and stouter bills than females, but proportionally shorter wings. Individual morphology influences flight energetics and hence the net energetic gain of foraging trips. Different flight modes (i.e. foraging techniques) require different aerodynamic specialisations and wing designs (Norberg 1990). For example, species with long wings, high aspect ratios (the ratio of wing span to mean wing chord), and low wing loadings have rather slow and inexpensive flight (Pennycuik 2008). It is generally assumed, however, that the sexual dimorphism in gulls is related to sex recognition or territorial defence (in which the bill plays an important role), rather than to feeding habits or range (Ingolfsson 1969).

The aim of this study was to investigate the relative importance of different individual foraging strategies, which would lead to the utilisation of distinct feeding habitats and area-specific resources within them. This is an important step in working towards understanding the consequences of different foraging strategies for reproductive success. We assumed that within the population of a generalist species, individual specialisation could reduce intra-specific competition and potentially increase individual fitness (c.f. Bolnick et al. 2003). In our study area, lesser black-backed gulls compete for prey with European herring gulls *Larus argentatus*. Given the suggestions by Smith (1966) on the effects of sympatric breeding and the suggestions expressed by Ingolfsson (1969) on sexual dimorphism being more related to sex recognition or territorial defence, we expected no or only minor differences in

Fig. 1 Cartographic representation of long trips aggregated per sex and breeding phase. Colours represent relative time spent within $2^{\circ}\text{N} \times 3^{\circ}\text{E}$ cells ($\times 100$ time in grid cell/cumulative time for all individuals in relevant breeding phase; considering only long trips). **a** Males egg phase, **b** females egg phase, **c** males chick phase, **d** females chick phase, **e** males that failed as breeders, **f** failed females. For each map, the number of individual birds, the number of long trips, and the total time (h) for all individuals combined are indicated in the upper-left corner. The colony location is indicated with an asterisk. Longitude and latitude are given in decimal degrees, and all maps have the same extent and resolution

foraging behaviour between males and females, despite the size differences between both sexes. Nevertheless, sexually distinct foraging strategies have been observed in several species of seabirds (González-Solís et al. 2000; Phillips et al. 2004), including taxa that are not sexually dimorphic (Lewis et al. 2002, 2005). We therefore investigated whether foraging behaviour was related to body size or sex.

We planned to study individual foraging strategies and dietary specialisations from time spent in particular foraging habitats and from common and characteristic prey types encountered at the nest sites. We expected breeding status (e.g. incubation or chick care) to influence prey choice and the time available for foraging activities. We studied the diet of lesser black-backed gulls from regurgitated matter found around the nests within the colony. To monitor the foraging activities and feeding habitats, 34 lesser black-backed gulls were instrumented with GPS tracking devices. The tracking information was combined with the breeding status and morphometric measurements of these individuals.

Methods

The study was based on a breeding colony on the Island Texel (The Netherlands, $53^{\circ}00'\text{N}$, $04^{\circ}43'\text{E}$) at the crossroads of the western Wadden Sea and the southern North Sea (Fig. 1). Within the study area, approximately 11,500 pairs of lesser black-backed gulls are breeding. Considering prey remains found at breeding territories, the main foraging areas for this population include open sea, grasslands, and arable land (Camphuysen et al. 2008; Camphuysen 2013). Data were collected from April to August in four consecutive breeding seasons (2008–2011) and pooled given that the overall diet did not differ between seasons, and that the tracking data revealed between-year consistency in the areas utilised by the birds.

Breeding data

We monitored the breeding status of tracked birds and the development of their chicks throughout the tracking period in comparison with a control population. A total of 100

nests were marked during egg laying each year. Marked nests were visited every third day throughout the breeding season (laying to hatching), and a randomly selected subset (c. 30–40 nests) was enclosed and monitored to assess chick growth and fledgling rates (Camphuysen 2013). Nests in which one of the partners was tracked with GPS loggers (see below) were also followed until fledgling by using enclosures. Breeding phases used in this study were (1) incubation and hatching (“egg phase”), (2) chick care until fledgling (first 45 days after hatching; “chick phase”), and (3) failed breeding (from the day an individual lost its clutch or brood, to the day it was last recorded in the colony within a single breeding season; “failed breeders”).

GPS tracking

A total of 34 breeding adult gulls (18 males, 16 females; Online Resource 1) were tracked using UvA-BiTS GPS loggers (Bouten et al. 2013). Individuals were trapped at marked nests half-way through incubation, using a walk in trap. Each bird was sexed on the basis biometrics (head plus bill length) with only 5 % expected misidentification (Coulson et al. 1983). We have no evidence that any of the tracked birds were wrongly sexed (from observations of sexual behaviour within the colony during the study period and in later years, *personal observations*). Other measurements included bill depth (at base, 0.1 mm), tarsus (mm), wing length (mm), and body mass (g). The mean body mass of tagged females amounted to 776 ± 63 g and that of males to 941 ± 53 g. The birds were colour ringed and an 18-g solar-powered GPS logger was mounted with a 3-g non-flexible Teflon harness on the back of the bird. The GPS logger and harness weighed less than 4 % of the body mass of the birds (average mass of logger and harness combined 2.7 % of female body mass, 2.2 % of male body mass). Birds were released immediately after being instrumented, which was usually within 20 min after catching. The tracking system enables changing the measurement frequency while the logger is on the bird. In general, a GPS location was taken every 5–20 min during the entire breeding season, irrespective of habitat use. Gaps in the data occurred when the battery was not sufficiently recharged or the GPS timed out before a fix could be made.

Data processing

The time series of consecutive GPS locations were grouped into three types of activity bouts per individual bird: (1) “nest bouts”, (2) “short trips”, and (3) “long trips”. A nest bout was a continuous period within the colony (presence within a 150 m radius around the centre of the colony). Bathing places and roosts occurred within c. 3 km around the study colony (identified from visual observations of

colour-ringed birds). Within this range, there are few suitable feeding opportunities except within the colony itself (e.g. gull chicks and eggs, cannibalism), or periodically in the surrounding dunes immediately surrounding the colony on insects and ripening berries. We defined a short trip as a period where an individual left the colony (moved out of the 150 m radius) but stayed within 3 km before returning to the colony. Finally long trips were defined as continuous periods where an individual left the colony and travelled further than 3 km before returning to the colony. As there are so few feeding opportunities within 3 km of the nest, foraging is associated almost exclusively with long trips. Any activity bouts with an interval of 60 min or more between two consecutive GPS locations were excluded from further analysis, in order to avoid potential bias when calculating time spent in a particular location. In addition, if the breeding status was uncertain for specific bouts, these were also removed from further analysis. In total, 6464 complete activity bouts were included in the analysis (3296 nest bouts, 1139 short trips, and 2029 long trips).

Potential foraging areas around the colony are (1) North Sea, including the coastal zone and beaches, (2) Wadden Sea, (3) Continental mainland areas (termed “mainland” throughout the text), and (4) the island Texel. Each individual GPS location was assigned to one of these four areas. The first two areas would provide marine or intertidal prey types, and the other two would provide terrestrial prey.

Data analysis

We calculated the time interval between consecutive GPS locations and associated this interval to the first GPS location. Using the time interval between consecutive GPS locations, we calculated the duration (h) of each activity bout as well as the proportion of time spent within each of the previously described habitats. For each long trip, we calculated the foraging range as the maximum (great circle) distance to the colony (km).

Using linear mixed-effects models (Pinheiro and Bates 2000), we tested the effect of sex and breeding status on the duration of nest bouts, short trips, long trips, and on the foraging range of long trips. The response variables were available per trip, and multiple trips were available per individual bird. The individual was treated as a random effect in the model, while the other predictor variables (sex and breeding status) were treated as fixed factors.

For each response variable, four models were evaluated:

1. a null model testing the effect of the individual (0)
2. a model testing the effect of the individual plus the effect of breeding status (b)
3. a model testing the effect of the individual plus the effect of sex (s)

4. a model testing the effect of the individual plus the effect of breeding status and sex (bs).

For nest bouts, a fifth model was evaluated as well:

5. a model as (4) but with an additional interaction term for sex and breeding status (bsx).

The models were ranked according to their corrected Akaike information criterion (AICc), and the Akaike weights were calculated to determine which model was best supported by the available data (Burnham and Anderson 2002). If a single model had an Akaike weight higher than 0.8, the alternative candidate models were disregarded. The best models were evaluated through a likelihood ratio test against the null model. In addition, the conditional R^2 values were calculated (Nakagawa and Schielzeth 2013). For the models that were considered a meaningful improvement over the null model, the model coefficients are reported along with 95 % confidence bounds. Full model results (including nonsignificant models) are reported in Online Resource 2. All calculations were conducted in R version 2.14.1 (R Development Core Team 2011; Pinheiro et al. 2012).

Differences in time allocation (h) per habitat between sexes were evaluated with the adjusted G -statistic (G_{adj} ; Sokal and Rohlf 1981) after summing the total time females and males spent on each habitat. Furthermore, to explore individual variability in the foraging behaviour during long trips and the potential effect of body size, we study the relationship between wing length (mm) and the mean individual foraging range (km) and trip duration (h) using linear models. We chose wing length, out of a number of collected biometrics, as a proxy for structural size and flight efficiency. We also compared the relationship between mean proportion (%) of time spent at sea or on land (%) to wing length (mm) using a generalised linear model with a logit transformation and a quasi-binomial link function. Comparisons with wing length were conducted for active breeding phases and failed breeding separately.

To compare the various response variables between breeding periods and between sexes, linear mixed-effects models with a random individual intercept were fitted using untransformed response variables, applying the lmer function from the lme4 package in R (Bates et al. 2014; R Core Team 2014). Subsequently the various models were compared by using the aictab function from the AICcmodavg package (Mazerolle 2014).

Linking diet and foraging areas

We inferred foraging strategies by combining information on the general diet composition of gulls at the colony level

with the habitats where these prey could be found. Tracking data were used to quantify where individuals spent their time. Diets were studied from spontaneously regurgitated matter (pellets, regurgitated indigestible food remains), from food boluses produced during handling of adults and chicks, and from chick-feed sub-sampled within the territories. During colony visits, marked territories were inspected for the presence of discarded prey items and each of these were individually bagged, numbered, and kept frozen for later analysis. Samples were not limited to tagged individuals. Between 2008 and 2011, a total of 3453 prey samples were collected (1517 during egg phase, 1877 during chick phase, 59 from failed breeders), containing 209 different prey types or prey species. Prey samples were analysed visually with a light microscope (Olympus SZ51), ensuring that even very small remains (such as earthworm setae, minute otoliths, and largely digested bread) were detected. With pellets, boluses, and regurgitated matter, some easily and fully digested prey was overlooked (e.g. white bread, ice cream, soft tissue invertebrates), but none of these soft prey types were considered important. The occurrence of prey types or prey species was expressed as frequency of occurrence (%) calculated over all samples (Barrett et al. 2007); a full analysis of the diet was beyond the scope of this contribution.

Results

Laying date, incubation period, and reproductive success

During our project (2008–2011), first eggs were found on 1 May $\pm$ 1.7 days (median egg laying 12 May $\pm$ 1.7 days), followed by an incubation period of 26.3 $\pm$ 0.7 days (n = 388 nests). The first hatchlings were recorded on 28 May $\pm$ 1.3 days (median hatching 8 June $\pm$ 1.4 days), the first fledglings (i.e. chicks at least 40 days of age) on 11 July $\pm$ 1.9 days (n = 180 nests). The hatching success in monitored control pairs amounted to 76.2 $\pm$ 0.06 % (n = 388 nests, 1101 eggs, SD calculated over four seasons). Hatching success in pairs in which one of the partners carried a GPS was 79.2 % (n = 32 nests, n = 109 eggs). Fledgling success in the Texel colony amounted to 0.53 $\pm$ 0.20 fledglings pair⁻¹ (n = 180 nests), and the reproductive success was again similar in pairs with a GPS-carrying individual (0.66 $\pm$ 0.85 fledglings pair⁻¹, n = 32 nests).

Nest bouts and short trips

The mean ($\pm$ SD) duration of nest bouts was 5.0 $\pm$ 4.8 h (n = 1339) for males and 3.7 $\pm$ 3.6 h (n = 1957) for females (Table 1). If breeding failed, both males and females continued to spend time at the nest, although less

Table 1 Mean duration of nest bouts, short trips, and long trips (h) and the range of long trips (km) in male and female lesser black-backed gulls during different breeding stages

	Egg phase	Chick phase	Failed breeders	Overall
Nest bouts (h)				
Male	7.3 ± 6.2	3.8 ± 3.4	4.9 ± 4.4	5.0 ± 4.8
<i>n</i>	387	698	254	1339
Female	5.4 ± 4.7	3.0 ± 2.8	3.4 ± 3.3	3.7 ± 3.6
<i>n</i>	514	1008	435	1957
	6.2 ± 5.5	3.3 ± 3.1	3.9 ± 3.8	
Short trip duration (h)				
Male	0.8 ± 0.9	0.9 ± 1.2	0.8 ± 1.1	0.9 ± 1.1
<i>n</i>	143	200	98	441
Female	0.9 ± 0.7	1.0 ± 0.9	1.1 ± 1.4	1.0 ± 1.1
<i>n</i>	158	293	247	698
	0.9 ± 0.8	1.0 ± 1.0	1.0 ± 1.3	
Long trip duration (h)				
Male	8.4 ± 9.0	6.7 ± 7.5	13.6 ± 16.1	8.3 ± 10.2
<i>n</i>	217	479	144	840
Female	6.0 ± 5.4	5.6 ± 9.4	13.3 ± 22.7	6.9 ± 11.9
<i>n</i>	325	688	176	1189
	7.0 ± 7.1	6.1 ± 8.7	13.4 ± 20.0	
Long trip range (km)				
Male	30.6 ± 37.2	32.6 ± 21.4	32.4 ± 26.0	32.0 ± 27.1
<i>n</i>	217	479	144	840
Female	17.2 ± 12.8	21.0 ± 23.1	27.0 ± 51.9	20.8 ± 27.6
<i>n</i>	325	688	176	1189
	22.6 ± 26.4	25.7 ± 23.1	29.4 ± 42.3	

Values are mean ± SD and sample size (*n*)

than in the egg phase and a bit more per visit than in the chick phase. The model selection procedure revealed that model 5 (a complete model with sex and breeding status as predictors) was most consistent with the data. All terms in this model were highly significant. Males spent significantly more time at the nest per visit than females—especially when breeding failed (hence the interaction effect). Nest bouts in the egg phase were longer than in the chick phase and failed breeding (see Table 2 for model coefficients, 0.95 confidence intervals, conditional R^2 and model P value). The mean duration of short trips (assumed to be trips to roosts) was 0.9 ± 1.0 h for males ($n = 441$) and 1.0 ± 1.1 h for females ($n = 698$; Table 1). There was no significant effect of sex or breeding status on the duration of short trips (Online Resource 2).

Long trips

The main characteristics of long trips (assumed to be foraging trips) are summarised in Table 1. Taking all long trips together ($n = 2029$), the 95 percentiles for duration and

range were 12 h and 47 min and 60.5 km from the nest, respectively. Mean duration and range of long trips were 8.3 ± 10.2 h and 6.9 ± 11.9 h in females; and the mean range of long trips was 32.0 ± 27.1 km in males ($n = 840$) and 20.8 ± 27.6 km in females ($n = 1189$; Table 1). The linear mixed model revealed that breeding status, but not sex, had a significant effect on the duration of long trips (Table 2). During active breeding, trip duration was significantly longer in the egg phase compared to the chick phase. The linear mixed model for foraging range revealed that the combined effect of sex and breeding status was significant at the 0.05 level (Table 2). In all breeding phases, males travelled significantly further than females and both sexes travelled further in the chick phase than in the egg phase.

Foraging areas and habitat use

Foraging areas were mainly to the southwest (North Sea), south (North Sea and terrestrial areas), southeast (Wadden Sea and terrestrial areas), and east of the colony on the Island Texel (Fig. 1). The proportion of time spent in different habitats on long trips varied between individuals representing a continuum of habitat use from almost exclusively terrestrial to almost exclusively marine (Fig. 2). The proportion of time spent in the main habitats was significantly different between the sexes, during breeding (egg phase: $G_{\text{adj}} = 1211.5$, $df = 3$, $P < 0.001$; chick phase: $G_{\text{adj}} = 1611.8$, $df = 3$, $P < 0.001$) as well as when comparing failed breeders ($G_{\text{adj}} = 910.8$, $df = 3$, $P < 0.001$). Males spent between two-thirds and three quarters of their time at sea (North Sea), whereas females divided their time between each of the main habitats (Table 3). Actively breeding females spent, in total, half of their foraging time within the Wadden Sea area: partly in the Wadden Sea itself (21 % in the egg phase, 25 % in the chick phase), partly on Wadden Sea Island Texel (resp. 29 and 24 %). Seven females that had lost either clutch or chicks substantially increased the time spent on terrestrial habitats on the mainland during long trips (56 % relative to 16 % when still actively breeding) and reduced their time spent within the Wadden Sea, on Texel and at the North Sea ($G_{\text{adj}} = 448.1$, $df = 3$, $P < 0.001$). Six males that had failed as breeders spent less time at the North Sea and somewhat increased their time in terrestrial areas (mainland and Texel; $G_{\text{adj}} = 59.9$, $df = 3$, $P < 0.001$) in comparison with the time spent in each habitat while still actively breeding. Males spent little time in the Wadden Sea during active breeding (4 %) and after failing (3 %; Fig. 1; Table 3).

Relationship between wing morphology and foraging trip characteristics

In active breeding birds, significant positive relations were found between wing length and mean duration of long trips

Table 2 Parameter values with 0.95 confidence intervals, conditional R^2 , P value, and explained deviance resulting from linear mixed models on the combined effect of sex and breeding status on foraging trip characteristics and the duration of nest bouts

	Parameter value (0.95 % CI)
(a) Duration of nest bouts (h)	
Male—egg phase	7.1 (5.6–8.7)
Male—chick phase	4.5 (2.6–6.4)
Male—failed breeders	5.5 (2.6–8.4)
Female—egg phase	5.7 (5.0–6.3)
Female—chick phase	3.0 (2.0–4.0)
Female—failed breeders	3.12 (1.9–4.3)
Conditional $R^2 = 0.18$	$P < 2.2\text{e}-16$
Explained dev. = 0.014	
Dispersion parameter = 3.9	
(b) Duration of foraging trips (h)	
Egg phase	7.6 (6.2–9.0)
Chick phase	6.6 (4.1–9.2)
Failed breeders	14.2 (11.2–17.3)
Conditional $R^2 = 0.12$	$P < 2.2\text{e}-16$
Explained dev. = 0.005	
Dispersion parameter = 10.6	
(c) Range of foraging trips (km)	
Female—egg phase	18.8 (14.7–22.9)
Female—chick phase	21.7 (14.7–28.7)
Female—failed breeders	27.7 (19.5–36.0)
Male—egg phase	29.3 (19.9–38.8)
Male—chick phase	32.2 (19.9–44.6)
Male—failed breeders	38.3 (24.7–51.9)
Conditional $R^2 = 0.10$	$P = 5.56\text{e}-07$
Explained dev. = 0.002	
Dispersion parameter = 26.6	

Only significant models are listed in this table (for all models that were evaluated, see Online Resource 2). Both predictor variables (gender and breeding status) are categorical, hence the parameters represent effect sizes. (a) Duration of nest bouts, (b) duration of foraging trips (this model only includes breeding status, sex was not significant), and (c) foraging trip range

(LM, $F_{1,32} = 7.52$, $P < 0.01$; Fig. 3a) and mean foraging range (LM, $F_{1,32} = 23.78$, $P < 0.001$; Fig. 3b). No relations were found between wing length and mean duration of long trips (LM, $F_{1,11} = 0.2639$, $P = 0.618$) or mean foraging range (LM, $F_{1,11} = 0.0145$, $P = 0.906$) in failed breeding birds. In active breeding birds, a significant positive relation was found between wing length and the proportion of time spent at sea during long trips (GLM, $F_{1,32} = 33.24$, $P < 0.001$; Fig. 3c) and there was a significant negative relation between wing length and the proportion of time spent in terrestrial habitats (i.e. mainland and Texel) (GLM, $F_{1,32} = 16.27$, $P < 0.001$; Fig. 3d). For failed breeders, no significant relations were found between wing length

(GLM, $F_{1,11} = 3.6022$, $P = 0.084$) and proportion of time at sea or on land (GLM, $F_{1,11} = 0.637$, $P = 0.441$).

Linking diet to foraging areas

Food samples ($n = 3453$) usually revealed a mix of species or prey types, probably of different origin. Overall, 87 % of all prey samples contained at least some prey of marine origin, and the diet of lesser black-backed gulls breeding at Texel was dominated by demersal North Sea fish, pelagic Nereid worms (mostly *Nereis longissima*), and the crustacean *Liocarcinus holsatus* (Online Resource 3). Given the species composition, most fish must have been obtained while competing for discards behind beam trawlers (discarded fish found in 77 % of all prey samples, frequency of occurrence of all marine fish 83 %; $n = 3453$). Prey from intertidal resources was rare (represented in 2 % of the samples, $n = 3453$): few intertidal crustaceans, polychaetes, and bivalves were encountered (Online Resource 3). On land, the diet and expected foraging conditions are considerably more variable. Prey types from terrestrial sources were found in 33 % of all prey samples. The most frequently encountered terrestrial prey were insects, plant material, gull chicks and eggs, and earthworms *Lubricus terrestris* (Online Resource 3).

The frequency of occurrence of marine prey (87 %) in the diet was high, as could be expected from the time spent by the tagged birds in the North Sea on long trips (Online Resource 3; Table 3). In contrast, the amount of intertidal prey (2 %) was much smaller than anticipated from the considerable time spent, notably by females, in the Wadden Sea (20–25 % of foraging time; Table 3).

Discussion

Tracking studies potentially suffer from logger effects, compromising the behaviour and survival of tagged individuals (Phillips et al. 2003; Igual et al. 2005). Our tags were always added in the egg phase when the birds were confidently incubating. We measured hatching success and fledgling rates within the colony at large (control pairs) and in pairs in which one of the partners was tracked with a GPS logger. Two pairs failed almost immediately after tagging (the tagged bird disappeared or died), and these results were not included in the present study. For the remaining birds, the highly similar breeding results in comparison with control pairs are seen as evidence that both groups performed equally well. We believe that the instrumentation has not influenced our results such that the outcomes are unreliable.

Levels of parental investment are the product of a simultaneous resolution of conflicts of interest between parents

Fig. 2 Individual time spent (%) on long trips during active breeding (egg or chick phase) in each of four main habitats (North Sea–NSea, Wadden Sea–WSea, terrestrial areas–Mainland, and the island Texel–Texel), sorted from left to right by sex (m → f) and by a decreasing

amount of time spent in the North Sea within each sex. Colour-ring codes (x axis) of females start with F, males start with M ($n = 34$ individuals, 2029 foraging trips, 2008–2011)

Table 3 Per cent of time spent by males and females in the four main habitats during foraging trips, within each breeding phase

	Egg phase		Chick phase		Failed breeders	
	Males (%)	Females (%)	Males (%)	Females (%)	Males (%)	Females (%)
% North Sea	78.4	28.6	65.4	36.9	66.4	22.6
% Mainland	13.6	21.2	24.9	14.2	21.0	56.4
% Texel	4.5	29.3	4.6	23.7	9.4	11.5
% Wadden Sea	3.6	21.0	5.1	25.2	3.3	9.5

Fig. 3 Long trip characteristics versus wing length (mm, as proxy for structural size) and sex of individual lesser black-backed gulls carrying GPS loggers as active breeding birds (2008–2011). **a** Mean trip duration (h; LM, $F_{1,32} = 7.75$, $P = 8.9421e-3$), **b** mean range (km; LM, $F_{1,32} = 25.42$, $P = 1.76e-5$), **c** proportion of time on the North Sea (GLM, $F_{1,32} = 33.22$, $P = 2.2e-6$), **d** proportion of time on land (mainland and Texel combined; GLM, $F_{1,32} = 16.05$, $P = 3.441e-4$). Males indicated with filled symbols, females with open symbols ($n = 34$ individuals, 2029 foraging trips). Solid lines are predictions from linear (a, b) and generalised linear models (c, d), exact P values are indicated for each plot

and offspring (survival, fitness; Royle et al. 2004). We therefore had expected that, due to a trade-off between the amount of time allocated to different activities such as self-provisioning, chick provisioning, and chick care, certain characteristics of foraging behaviour would change in the course of a season. The results of the mixed models showed that in the chick phase, the duration of trips and nest visits declined, indicating that both males and females made more frequent visits to the nest to provision the offspring. More frequent foraging trips suggest an increase in foraging effort, likely in response to increasing energetic demands of the developing chicks (Drent and Daan 1980). Similar changes in behaviour between different stages of the breeding season have been noted in other seabirds (Clarke et al. 1998; Phillips et al. 2004; Paiva et al. 2008). The tracking data also showed that males spent relatively more time in the breeding territory than females. This could either mean that males spent more time in nest or chick defence than females, or that the presence at the territory is important for males to safeguard their chosen site for future breeding opportunities within the colony (Morse Nice 1941; Hinde 1956). A marked increase in nest-bout duration in males of which the breeding attempt had failed is consistent with the latter hypothesis.

It appeared that the foraging activities (long trips) of lesser black-backed gulls from Texel were concentrated within 60 km around the colony, but that the foraging habitat used varied between individuals from almost completely terrestrial to completely marine (Fig. 2). Overall, active breeders spent 67 % of their time on long trips in marine habitats and 34 % in terrestrial areas. Contrary to our expectations, some aspects of the foraging behaviour differed more or less consistently between the sexes. Males spent significantly more time and further out in the open North Sea than females. It were females rather than males that utilised terrestrial resources on Texel and that foraged substantial amounts of time within the Wadden Sea. The structural size of the birds may at least in part have influenced the individual specialisation in habitat choice. The proportion of time spent at sea, trip duration, and trip range all increased significantly with increasing wing length, suggesting that larger (male) birds may be more fit to the energetically more demanding, more competitive job far out at sea. Morphology, especially mass, wing load, and aspect ratio, has important consequences for flight performance and flight energetics with cruising flight speeds and energy expenditure scaling with mass and wing load (Norberg 1990; Alerstam et al. 2007; Pennycuik 2008). Wind speeds at sea are often higher than over land, already close to the surface, due to the low surface roughness at sea (Stull 1988). Thus, birds with higher cruising speeds may have an advantage at sea because they could compensate for a broader range of wind conditions (Chapman et al. 2011).

The marine orientation, found in our tracking studies, could also be deduced from the prey samples collected in the colony. It was from these samples that prey species could be identified, showing that most of the marine prey were demersal fish species, many of which are normally only available to lesser black-backed gulls as discards behind beam trawlers, the predominant offshore trawling fishery in this part of the North Sea (van Beek et al. 1990; Camphuysen 1994). Other marine prey include *Liocarcinus holsatus* and Nereid worms (as epitoky; Probst 1933) that both have an ephemeral, but frequent occurrence at the sea surface in the North Sea and that are captured by shallow plunge-diving (Gallien 1936; Schwemmer and Garthe 2005). The absence of intertidal prey items in the samples collected at Texel was striking given the time spent by tracked birds within the Wadden Sea. The Wadden Sea is internationally known as a major stop-over site for millions of migrants that feed on invertebrate prey on mudflats at low tide (Van de Kam et al. 1999). It was later found (from the same tracking data) that the gulls focused almost exclusively on deeper gullies and avoided mudflats and shallow parts of the Wadden Sea that fall dry at low tide (Tyson et al. 2014). The concentration on deeper gullies implied that the birds focused on pelagic prey or on discards produced by shrimpers within these gullies. Bottom trawling for shrimps is the predominant fishery in the Wadden Sea, and the discarded fish are similar species, but often smaller in size, than discarded fish that is available at the large offshore beam trawlers targeting Sole *Solea solea* and Plaice *Pleuronectes platessa* (Tiews 1978; Walter 1997). The analysis of prey samples collected in the colony had thus far only hinted at the exploitation of fishing vessels in the Wadden Sea (the presence of *Crangon crangon* and juvenile flatfish; Camphuysen et al. 2008).

A difference in habitat use between the sexes could imply habitat or niche segregation at the macro-scale and our findings present evidence for both. It were only female lesser black-backed gulls that utilised resources within the Wadden Sea for substantial amounts of time, it were females that foraged much time on land, and it were mostly males that foraged most of their time on the open North Sea. Differences between sexes might be considered ends along a continuum of individual variation in foraging behaviour (Bolnick et al. 2003). While studies of resource use and population dynamics often treat conspecific individuals as ecologically equivalent, individual specialisation has been shown in a large range of species distributed across a broad range of taxonomic groups (Clarke et al. 1998; Conradt et al. 1999; Shaffer et al. 2001). A diverse array of physiological, behavioural, and ecological mechanisms could generate intra-population variation and between-individual variation in some cases may comprise the majority of the population's niche width (Bolnick et al.

2003). Sexual differences in foraging behaviour of parents have been observed in a number of sexually size-dimorphic animals, with the usual inference that sex-specific differences are mediated primarily by differences in body size (González-Solís et al. 2000; Phillips et al. 2004).

Overall body size could be an aspect of importance driving sexual segregation in foraging habitats and foraging specialisation. Scavenging at offshore fishing vessels involves intense inter- and intra-specific competition (Furness et al. 1988; Camphuysen 1995). Large, powerful seabirds generally forage more optimally under these conditions than smaller ones (Hudson 1989; Camphuysen et al. 1995), which could explain the more extensive use of marine resources (beam trawlers) by larger males than by smaller females. With larger seabirds foraging with greater success at trawlers, the observed differences in resource utilisation between male and female lesser black-backed gulls may be driven by differences in physiological performance (i.e. size-mediated differences in foraging success in a competitive setting). However, while offshore trawlers (in summer) in the Southern North Sea are traditionally the domain of lesser black-backed gulls with few inter-specific competitors of equal size and strength (Camphuysen 1995), flocks of scavenging seabirds associated with near-shore shrimp trawlers, certainly those within the Wadden Sea, are numerically dominated by larger, more powerful herring gulls (Walter and Becker 1994; Camphuysen et al. 1995). In other words, the female lesser black-backed gulls utilising shrimpers in the Wadden Sea faced (and would normally be outnumbered by) even stronger competitors than they would when they joined male conspecifics at offshore beam trawlers. A higher manoeuvrability of the small and relatively slender female lesser black-backed gulls facing herring gulls around moving nearshore trawlers could be beneficial for them (cf. Strann and Vader 1992). This suggestion would need to be confirmed in an experimental setup (cf. Camphuysen et al. 1995).

Foraging on land, predominantly by female lesser black-backed gulls in this study, requires rather different skills. Several of the most frequently encountered prey items (Online Resource 3; Camphuysen et al. 2008, 2010) are not normally captured during mass feeding frenzies under stress from strong inter- or intra-specific competition that would require particular competitive strength. Most natural prey items on land may be taken rather opportunistically, under the influence of particular weather conditions (insects, earthworms), seasonal trends (ripening fruits), or agricultural activities (small mammals, cereals, insects, worms; Camphuysen 2013), or with hit-and-run techniques (snatching away prey in urbanised areas). Anthropogenic resources included landfills (waste disposal), sewage plants (water treatment), and urban areas. Small feeding frenzies are formed in some of these, but with abundant

opportunities for profitable feeding for smaller, more manoeuvrable, less competitive birds (Greig et al. 1985; Rock 2005).

The differences in foraging behaviour, foraging areas, and prey obtained in these areas suggest that in general, males and females provision for their young differently. Sexual differences in parental care, foraging behaviour, and food provisioning in some seabirds are well known but poorly understood. These differences cannot always be attributed to sexual dimorphism (Lewis et al. 2002) but may for example point at alternative foraging strategies and resource allocation by males and females (Weimerskirch et al. 1997; Clarke et al. 1998; Thaxter et al. 2009). These and other findings (examples listed in Elliott et al. 2010) highlight the need to investigate sexual differences in the foraging behaviour of seabirds and other species more closely. Testing alternative hypotheses that do not rely only on differences in body size such as hypotheses on differential parental investment could provide better explanations of the observed differences between the sexes. Elliott et al. (2010), for example, proposed that risk partitioning may contribute to the prevalence of sex-specific behaviours in monomorphic animals and that patterns are likely context specific rather than species specific. The use of different behavioural strategies by each parent may increase reproductive success for both partners through risk partitioning. Elliott et al. (2010) showed that in Brünnich's Guillemots *Uria lomvia*, chick-provisioning males were feeding on "risk-averse" prey (consistent across time and space), whereas females fed on "risk-prone" prey. Models indicated that mixed-risk pairs had higher success than "risky" or "riskless" pairs. A similar scenario could be true for lesser black-backed gulls, where the more powerful males feed in a strongly competitive setting at sea (Furness et al. 1992) with few alternative resources nearby ("risk prone"), but primarily females utilised fishing fleets nearer the colony, with a whole suite of alternative foraging opportunities nearby on land ("risk averse"). While sex and breeding status influence foraging strategies to some extent, much of the unexplained variation in foraging behaviour is likely due to individual specialisation in prey choice. The combination of individual specialisation and sexual segregation during the breeding season may reduce intra-specific competition, competition between the sexes (and hence within a pair), or alternatively, reduce the risk of unbalanced food provisioning, neither of which are mutually exclusive.

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