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Flight and foraging patterns of lesser black-backed gulls and northern gannets in the southern North Sea

Dissertation

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Der Dekan

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SUMMARY

The currently increasing human-animal competition for marine resources in terms of food and space use requires sophisticated management and conservation plans to secure sufficient retreats for marine wildlife such as seabirds. Therefore, knowledge of the spatiotemporal habitat utilization of seabirds is crucial for identifying key areas which are used for e.g. foraging or resting. In this thesis, two common seabird species, lesser black-backed gulls *Larus fuscus* and northern gannets *Morus bassanus*, were chosen as models to analyse their flight and foraging patterns during the breeding periods. The primary aim was to account for colony-specific, sex-specific, but also individual differences in the spatiotemporal habitat utilization of incubating lesser black-backed gulls breeding at different colonies along the German North Sea Coast, and to examine the effect of offshore wind farms – a recent and increasing anthropogenic pressure on the marine environment – on the vertical (lesser black-backed gulls) and horizontal (northern gannets) space use of both model species.

The main methods employed to analyse the birds' foraging patterns were GPS telemetry, and diet analyses of pellet and blood samples (stable isotope analysis). GPS data loggers were attached to individual birds which were captured on their nests during incubation. Lesser black-backed gulls (overall n = 79, successfully recaptured with sufficient data) were caught at the breeding colonies Borkum, Juist, Norderney, Spiekeroog, Amrum and Helgoland, varying in size and distance to the mainland coast. Northern gannets (n = 3, successfully recaptured with sufficient data) were caught at the only German breeding colony Helgoland. The recorded data helped to identify the foraging trips of each individual during a period of several days to several weeks. Combined with pellet analyses and stable isotope mixing models, tracking data should reveal a comprehensive overview of the spatiotemporal distribution and the foraging ecology of the study species. The foraging-trip characteristics (e.g. duration, length, habitat type, flight height) were used in various statistical models (primarily linear mixed models) to examine the above-mentioned study aims.

Lesser-black backed gulls fed at both the marine and the terrestrial habitat. The extent to which the birds utilized these habitat types varied among the breeding colonies. All colony-specific foraging trips were spatially segregated, and could primarily be related to the relevant colony size. For instance, the larger the breeding colony, the farther and longer the foraging trips conducted by the individuals. A closer look at the level of sexes also revealed spatial segregation in foraging habitats. Females tended to forage in terrestrial habitats, while males foraged rather in the marine environment. Stable isotope analysis supported this finding, though sex-specific trophic segregation was not distinct. Accounting for individual factors such as stress level or body mass, unravelled the sex-specific foraging strategies and demonstrated a complex within-sex interaction of both parameters. This indicates that birds cope differently with stress dependent on the individual body mass.

The vertical space use of lesser black-backed gulls differed between terrestrial and marine foraging trips, trips at night and during the day, and between different flight types (straight commuting versus tortuous foraging flights). Regarding the impact of offshore wind farms, they overlapped with the dangerous rotor swept area, and thus were under risk of collision to a certain extent, but they did not show any avoidance of the wind farm areas. In contrast, northern gannets clearly flew detours around wind farms with turbines already installed. This avoidance behaviour will lead to a large amount of habitat loss along with the increasing construction of wind farms in the German Bight. The two opposing behaviours of the study species towards offshore wind farms are amongst others due to their different flight manoeuvrability and thus their sensitivity to vertical obstacles along their flight routes to lucrative foraging sites.

In summary, this thesis gives novel and comprehensive insights into the foraging ecology and the habitat utilization of lesser black-backed gulls at the population level and the level of sexes, and indicates the presence of individual specialization in this generalist species. It corroborates the role of reducing intraspecific competition at each level of consideration. In relation to offshore wind farms, this thesis revealed important information of the vertical space use of lesser black-backed gulls, and furthermore provides first indications of a clear avoidance of these areas in northern gannets. These findings will not only have implications for the future marine spatial planning, but will also be relevant in terms of management and conservation plans for seabirds in the southern North Sea.

ZUSAMMENFASSUNG

Die wachsende Konkurrenz zwischen Mensch und Tier um marine Ressourcen wie Nahrung und Raumnutzung erfordert komplexe Management- und Naturschutzpläne, die ausreichend Rückzugsgebiete für die marine Tierwelt, wie z.B. Seevögel, sicherstellen. Hierfür sind genaue Kenntnisse der räumlichen und zeitlichen Habitatnutzung von Seevögeln essentiell. So können Kerngebiete, die zur Nahrungssuche oder Rast genutzt werden, identifiziert werden.

In der vorliegenden Arbeit wurden Heringsmöwen (*Larus fuscus*) und Basstölpel (*Morus bassanus*) als Modellarten ausgewählt, um deren Flug- und Nahrungssuchmuster während der Brutzeit zu analysieren. Das primäre Ziel dieser Studie war die Analyse der raumzeitlichen Habitatnutzung brütender Heringsmöwen hinsichtlich möglicher Unterschiede zwischen den einzelnen Brutkolonien entlang der deutschen Nordseeküste, den Geschlechtern, sowie den einzelnen Individuen. Weiterhin sollten mögliche Effekte von Offshore-Windparks, die einen aktuellen und wachsenden Druck auf die marine Umwelt darstellen, auf die vertikale (Heringsmöwen) und horizontale (Basstölpel) Raumnutzung beider Modellarten untersucht werden.

Die Nahrungssuchmuster beider Arten wurden mit Hilfe von GPS-Telemetrie und Nahrungsanalysen anhand von gesammelten Speiballen und Blutproben (Analyse stabiler Isotope) analysiert. Um die GPS-Datenlogger an den Vögeln anbringen zu können wurden diese mit Hilfe von Kastenfallen auf ihrem Nest gefangen. Heringsmöwen (*n* = 79, erfolgreich wiedergefangen mit ausreichend aufgezeichneten Daten) wurden in den Brutkolonien Borkum, Juist, Norderney, Spiekeroog, Amrum und Helgoland gefangen, die alle in Größe und Lage zum Festland variierten. Basstölpel (*n* = 3, erfolgreich wiedergefangen mit ausreichend aufgezeichneten Daten) wurden in der einzigen deutschen Brutkolonie auf Helgoland gefangen. Mit Hilfe der aufgezeichneten Daten konnten die einzelnen Nahrungsflüge der Tiere über einen Zeitraum von einigen Tagen bis zu mehreren Wochen identifiziert werden. Zusammen mit den Nahrungsanalysen aus Speiballen und stabilen Isotopen (stable isotope mixing models) können die Telemetrie-Daten einen umfassenden Überblick der raumzeitlichen Verbreitung sowie der Nahrungsökologie beider Untersuchungsarten liefern. Die Kennzeichen der Nahrungsflüge (z.B. Dauer, Länge, Habitattyp, Flughöhe) wurden anhand verschiedener statistischer Modelle (v.a. gemischte lineare Modelle) untersucht.

Heringsmöwen fraßen sowohl in terrestrischen als auch in marinen Habitaten. Je nach Brutkolonie wurden die beiden Habitattypen in unterschiedlichem Maße genutzt. Alle koloniespezifischen Nahrungsflüge waren räumlich voneinander getrennt und konnten primär auf die jeweilige Koloniegröße zurückgeführt werden. Beispielsweise waren die individuellen Nahrungsflüge zeitlich und räumlich länger, je größer die Brutkolonie war.

Die genauere Betrachtung der Geschlechter zeigte ebenfalls eine räumliche Trennung der Nahrungsflüge. Weibchen tendierten zu einer Nahrungssuche in terrestrischen Habitaten, während die Männchen sich eher auf das marine Habitat konzentrierten. Die Stabile-Isotopen-Analyse ergab ein ähnliches Ergebnis, wobei die Nahrung sich zwischen den Geschlechtern nicht so eindeutig unterschied. Mit Hinzunahme individueller Faktoren wie z.B. Stresslevel oder Gewicht konnten die geschlechtsspezifischen Nahrungssuchstrategien weiter aufgelöst werden. Diese Analysen ergaben komplexe Wechselwirkungen zwischen beiden Parametern innerhalb der Geschlechter, was auf einen unterschiedlichen Umgang mit Stress in Abhängigkeit von der individuellen Körpermasse hinweist.

Die vertikale Raumnutzung der Heringsmöwen unterschied sich je nach aufgesuchtem Habitattyp, Tageszeit und Flugweise (gerade Streckenflüge gegenüber kurvigen Nahrungsflügen). Bezogen auf die Auswirkungen von Offshore-Windparks überlappten die Flüge mit dem gefährlichen Rotorbereich der Anlagen, die Möwen waren demnach einem gewissen Kollisionsrisiko ausgesetzt. Allerdings zeigten sie keinerlei Meidungsverhalten gegenüber den Windparks. Im Gegensatz dazu umflogen die Basstölpel die Windparks mit bereits installierten Turbinen. Mit der Errichtung weiterer Windparks in der Deutschen Bucht wird dieses eindeutige Meidungsverhalten zu einem großflächigen Habitatverlust führen. Die beiden gegensätzlichen Verhaltensweisen der Untersuchungsarten gegenüber Windparks sind u.a. auf deren unterschiedliche Manövrierfähigkeit im Flug und somit deren unterschiedliche Sensitivität gegenüber vertikalen Bauwerken auf den Flugwegen zu lukrativen Nahrungsgründen zurückzuführen.

Die vorliegende Arbeit liefert neue und umfassende Einblicke in die Ernährungsökologie und die Habitatnutzung von Heringsmöwen auf Ebene der Population und der Geschlechter, und weist auf die Existenz individueller Spezialisierung in dieser Seevogelart hin. Die Ergebnisse betonen den hohen Stellenwert von Reduzierung bzw. Vermeidung intraspezifischer Konkurrenz auf verschiedenen Ebenen. Hinsichtlich der Offshore-Windparks liefert die Arbeit wichtige Daten zur vertikalen Raumnutzung von Heringsmöwen sowie erste Anzeichen eines eindeutigen Meidungsverhaltens von Basstölpeln. Diese Ergebnisse haben nicht nur Konsequenzen für die zukünftige marine Raumplanung, sondern auch für die Management- und Naturschutzpläne für Seevögel in der südlichen Nordsee.

GENERAL INTRODUCTION

Foraging ecology of seabirds

Seabirds as top predators play a key role in the marine ecosystem (Croxall 1987; Furness and Monaghan 1987; Schreiber and Burger 2001). They cover large distances to search for food and use a variety of resources at different trophic levels ranging from zooplankton to pelagic fish. They thus are one of the top-down forces in this environment. Simultaneously, they depend on food abundance (bottom-up control), which in turn might be associated with primary productivity and physical habitat features like fronts or upwelling zones (Ballance et al. 2001; Ballance et al. 2006; Grémillet et al. 2008a). The distribution of marine prey is patchy and scale-dependent, and due to its high mobility often hard to predict (Weimerskirch 2007; Fauchald 2009). The patchy structure of prey distribution varies over time and space, and exhibits a nested patch hierarchy hampering seabirds' foraging (Kotliar and Wiens 1990; Fauchald and Tveraa 2006; Weimerskirch 2007). They have thus evolved a variety of foraging strategies and behaviours to account for the complexity and unpredictability of prey distribution. Prey is localised by orientation on physical features or by associating with subsurface predators, which make the prey available for surface-feeding seabird species (Ashmole and Ashmole 1967; Ballance et al. 1997). Alternatively, they orientate on (multi-species) feeding flocks indicating the presence of prey (Porter and Sealy 1981; Ballance et al. 1997; Yen et al. 2004), or react to conspecifics starting for or returning from foraging flights (Thiebault et al. 2014). Foraging behaviour or feeding techniques, respectively, range from plunge (e.g. gannets, terns) or pursuit diving (e.g. auks, cormorants) to surface-feeding (e.g. gulls) and kleptoparasitism (e.g. skuas) (Nelson 1980).

The role of competition

Most of the seabird species are colonial breeders and central-place foragers during the breeding season (Coulson 2002). That means, competing for resources against conspecifics and other species breeding sympatrically at a time, when breeders are challenged to balance incubation or chick-rearing and self-provisioning, and constrained to forage within a certain radius around the colony (e.g. Wittenberger and Hunt 1985¸Croxall 1987). The intraspecific competition for food sources may lead to food depletion around the breeding sites and thus force the individuals to increase their foraging range (Ashmole 1963; Coulson 2002; Grémillet et al. 2004). Seabirds have evolved various avoidance strategies to deal with this disadvantage of colonial breeding: they use spatially segregated (in fact horizontally and vertically) foraging sites (Grémillet et al. 2004; Thaxter et al. 2009; Wakefield et al. 2013), forage at different times of day (Paredes et al. 2008), or use different types (trophic segregation) and/or sizes of prey (e.g. Bearhop et al. 2006). This resource partitioning in response to density-dependent competition can occur at both the colony (Grémillet et al. 2004; Wakefield et al. 2013) and the individual level between (Lewis et al. 2002; Thaxter et al. 2009), but also within sexes (Sommerfeld et al. 2013; Ratcliffe et al.

2013; Ceia et al. 2014a). Thus, individual foraging specialisation also plays a major role in seabird foraging ecology (e.g. Bolnick et al. 2003; Sargeant 2007).

Seabirds are often used as ecological indicators for changes in the marine environment, in particular in light of climate change and the increasing anthropogenic pressures on the marine ecosystem such as fisheries or offshore wind farms (e.g. Furness and Monaghan 1987; Piatt et al. 2007; reviewed in Durant et al. 2009). Their close relationship to the sea and their longevity make them well-suited model species to draw conclusions of the food availability, and more generally, to monitor the status of the marine ecosystem (Furness and Monaghan 1987; Furness and Camphuysen 1997; ICES 2003).

Seabirds confronted with offshore wind farms

There are several seabird-human interactions producing conflicts, e.g. fisheries, oil production, sand and gravel mining, and most recently offshore wind farms (Furness and Monaghan 1987; Montevecchi 2002; Furness et al. 2013). Generally, seabirds and humans compete for food resources and space or, from the seabirds' point of view, for (foraging) habitat. Several seabirds are sensitive to disturbance caused e.g. by shipping traffic or any offshore construction within their foraging habitat, which either forces them to fly detours around these constructions or represents a collision risk. Some seabird species are even attracted by anthropogenic activities at sea, e.g. scavenging behind fishing vessels (Garthe and Hüppop 2004; Votier et al. 2013; Bodey et al. 2014a).

The increasing development and construction of offshore wind farms throughout the EU has proceeded parallel to the recent debate about the necessary energy transition (EU Guidelines on State aid for Environmental Protection 2008; Environmental and Energy State Aid Guidelines EEAG 2014–2020, European Commission 2014), and the EU Renewable Energy Directive. In Germany, wind farm construction started in 2009. To date, there are four offshore wind farms operating, six under construction and 21 more approved (Fig. 1).

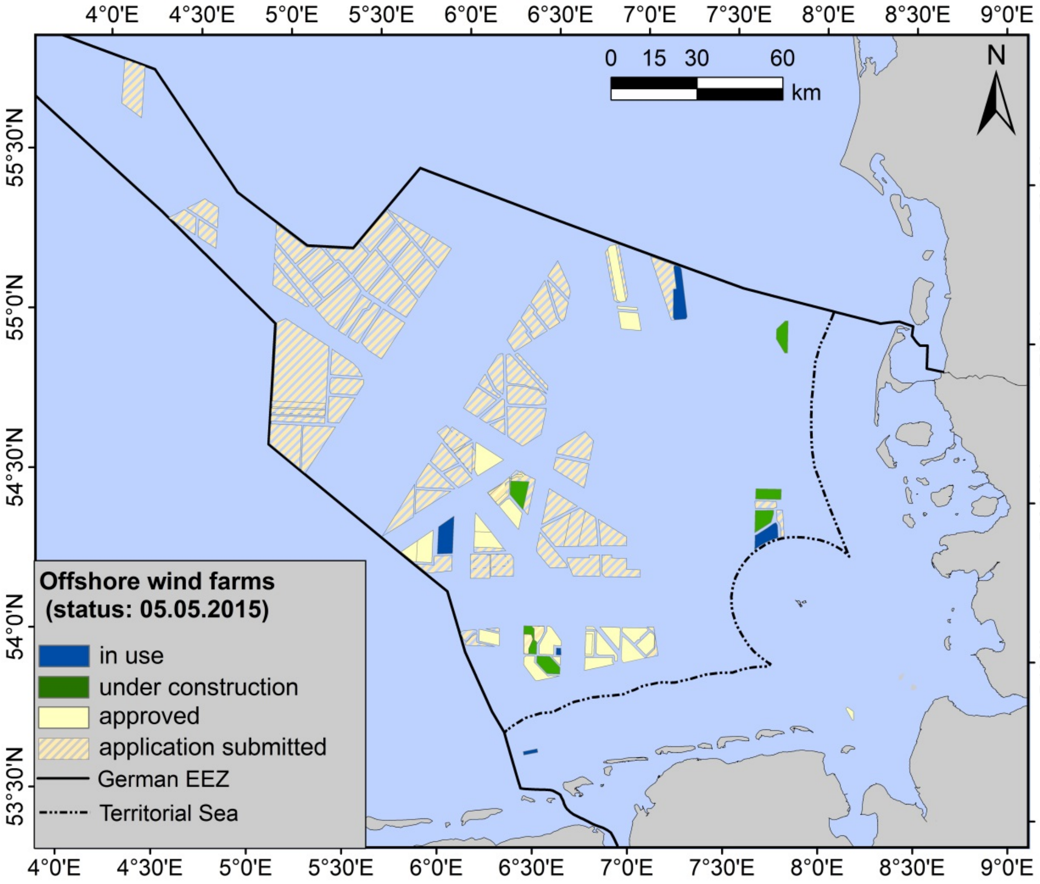

Fig. 1 Current status of offshore wind farms in the German EEZ (North Sea). Modified from Federal Maritime and Hydrographic Agency 2015 (http://www.bsh.de/en/Marine_uses/Industry/CONTIS_maps/NorthSeaOffshoreWindfarmsPilotProjects.pdf, status: 05.05.2015)

Mortality due to collision, habitat displacement or loss, dissection of commonly used flight routes, changes in benthic and pelagic habitat structure (e.g. emerging macrobenthic communities at the turbine foundations followed by changes of the whole prey community; Lindeboom et al. 2011) are known possible effects of offshore wind farms on seabirds (Garthe and Hüppop 2004; Furness et al. 2013; Thaxter et al. 2015). Garthe and Hüppop (2004) applied a first wind farm sensitivity index (WSI) for the southern North and the Baltic Seas to assess these effects. Divers (*Gavia* spp.) seem to be most sensitive to offshore wind farms, in particular with regard to the habitat displacement, while several gull species (*Larus* spp.) and northern gannets (*Morus bassanus*) are more likely to be collision-endangered (Furness et al. 2013).

GPS telemetry and stable isotope analysis as integrative approaches to study spatiotemporal and trophic patterns

Modern data loggers attached on seabirds offer high-resolution data of individual foraging patterns at sea over a certain time period (Wilson et al. 2002; Ropert-Coudert and Wilson 2005; Evans et al. 2013). The rapid development and miniaturisation of GPS devices allows the equipment of smaller and lighter species, and simultaneously a more or less permanent attachment (by solar panels; e.g. Bouten et al. 2013) with careful regard to the individuals' condition (Burger and Shaffer 2008; Barron et al. 2010; Vandenabeele et al. 2012). Recently, there is an increasing number of studies combining individual tracking data with dietary information derived from stable isotopes (Masello et al. 2010; Bodey et al. 2014b; Ceia et al. 2014b; Ceia et al. 2014a). Stable isotope analyses of carbon and nitrogen is a common tool to assess the diet, trophic interactions and habitat selection of seabirds (Inger and Bearhop 2008; Bond and Jones 2009). There are several studies deriving conservation and management implications of tracking and stable isotope data of seabirds (Bograd et al. 2010; Kowalczyk et al. 2014; Kowalczyk et al. 2015). The combination of both approaches enables a comprehensive insight into the foraging behaviour of individuals and populations. Moreover, both approaches are well-suited to monitor spatiotemporal and trophic relationships in the marine food web over a long time period.

Objectives and chapter outline

This thesis aims to analyse the flight and foraging patterns of different seabird species at the level of colonies (population) and individuals (sexes) during the breeding period. Habitat utilisation and trophic relationships are combined to provide a comprehensive picture of seabird foraging ecology in the southern North Sea. Moreover, these spatiotemporal patterns are considered in light of offshore wind farms, representing a recent anthropogenic pressure which affects the foraging and space use of various seabird species.

Two common seabird species with large-enough foraging ranges were used as models to achieve these objectives. First, the lesser black-backed gull (*Larus fuscus*) was chosen as representative of surface-feeding generalists utilising the marine as well as the terrestrial habitat for foraging. During breeding season, they are closely related to their breeding colonies along the German North Sea coast, but nevertheless most offshore distributed compared to the other larids of the study area (e.g. Mendel et al. 2008). This opportunistic species feeds on swimming crabs (*Liocarcinus* spp.), pelagic (e.g. *Sprattus sprattus, Clupea harengus*) or discarded fish (e.g. *Gadus morhua, Eutrigla gurnardus*), earthworms (Lumbricidae), insects or small mammals, and refuse (Camphuysen 1995; Kubetzki and Garthe 2003; Camphuysen et al. 2010). Lesser black-backed gulls do not only have a broad food spectrum, but are also flight generalists with a very manoeuvrable flight style allowing spontaneous evasive movements, when an obstacle occurs during flying (Camphuysen 1995; Klaassen et al. 2011; Shamoun-Baranes et al. 2011). Nevertheless, they are likely to collide with obstacles during poor visibility (Garthe and Hüppop 2004; Furness et al. 2013), especially because they seem to fly in the critical heights of the rotor swept area regularly (Cook et al. 2012; Garthe et al. 2012; Furness et al. 2013). Second, the northern gannet was chosen representing a plunge-diving piscivore with a wide-ranging offshore distribution in the southern North Sea (Mendel et al. 2008). This species mainly feeds on pelagic shoaling fish such as mackerels (*Scomber scombrus*) and herrings (*Clupea harengus*), but is able to switch to other fish species, when its main food resources occur in small quantities (Mitchell et al. 2004; Garthe et al. 2007; Garthe et al. 2014). In Germany, there is only one breeding colony of northern gannets at the offshore island Helgoland. Compared to e.g. lesser black-backed gulls, northern gannets are rather inflexible flyers, and thus particularly susceptible to collision with offshore wind farms (Garthe and Hüppop 2004; Mendel et al. 2008; Furness et al. 2013).

In particular, the following questions were addressed:

- How do lesser black-backed gulls generally forage, and how do they utilise their foraging habitat?
- How do lesser black-backed gulls deal with density-dependent, intraspecific competition?
- At which levels do spatial and/or trophic segregation occur?
- How do offshore wind farms affect the vertical and horizontal flight and foraging patterns of two seabird species differing in their flexibility to cope with man-made changes in the marine environment?

This thesis comprises four independent chapters to answer these questions. The two main methods applied were GPS tracking by attaching small data loggers on the individuals throughout the breeding period, and stable isotope analyses of nitrogen and carbon derived from individual blood samples to assess the birds' diet during the equipment period.

Chapter I deals with spatial segregation of incubating lesser black-backed gulls from six different breeding sites on the colony level aiming to identify colony-specific foraging patterns. In **Chapter II** sex-specific differences between lesser black-backed gulls from several breeding colonies are examined accounting for individual variations in body mass and stress level. The vertical space use of flying lesser black-backed gulls is analysed against the background of impact assessments of offshore wind farms, and compared among different flight destinations, times of day and flight types in **Chapter III**. **Chapter IV** examines foraging flights of northern gannets throughout the breeding season in light of offshore wind farms installed in close proximity to the breeding colony.

CHAPTER I:
Varying foraging patterns in response to competition? A multi-colony approach in a generalist seabird

Corman AM, Mendel B, Voigt CC, Garthe S (under review) Varying foraging patterns in response to competition? A multi-colony approach in a generalist seabird

Varying foraging patterns in response to competition? A multi-colony approach in a generalist seabird

Anna-Marie Corman, Bettina Mendel, Christian C. Voigt and Stefan Garthe

Abstract

Reducing resource competition is a crucial requirement for colonial seabirds to ensure adequate self- and chick-provisioning during breeding season. Spatial segregation is a common avoidance strategy among and within species from neighbouring breeding colonies.
We determined if the foraging behaviours of incubating lesser black-backed gulls (*Larus fuscus*) differed between six colonies varying in size and distance to mainland, and if any differences could be related to the foraging habitats visited.

Seventy-nine incubating individuals from six study colonies along the German North Sea coast were equipped with GPS data loggers in multiple years. Dietary information was gained by sampling food pellets, and blood samples were taken for stable isotope analyses.
Foraging patterns clearly differed among and within colonies. Foraging range increased with increasing colony size and decreased with increasing colony distance from the mainland, though the latter might be due to the inclusion of the only offshore colony. Gulls from larger colonies with consequently greater density-dependent competition were more likely to forage at land instead of at sea. The diets of the gulls from the colonies furthest from each other differed, while the diets from the other colonies overlapped with each other.

The spatial segregation and dietary similarities suggest that lesser black-backed gulls foraged at different sites and utilised two main habitat types, though these were similar across foraging areas for all colonies. The avoidance of intraspecific competition results in colony-specific foraging patterns, potentially causing more intensive utilization of terrestrial foraging sites, which may offer more predictable and easily available foraging compared with the marine environment.

Keywords foraging strategy, GPS tracking, intraspecific competition, *Larus fuscus*, stable isotope analyses, utilization distribution

Introduction

Colonial seabirds are central-place foragers during the breeding period, and therefore depend on continuous and sufficient availability of prey within accessible distances of their breeding colony (Wittenberger and Hunt 1985). Optimal foraging theory suggests that animals should use the minimum traveling distances necessary to satisfy their energy demands (Schoener 1971). Visiting more distant sites will thus only be profitable if the prey is of higher quality, more abundant or more easily available than at sites closer to the colony (Houston and

McNamara 1985; Harding et al. 2013). Density-dependent competition, both within and between adjacent colonies with overlapping foraging ranges, represents another limiting factor for colonial breeders (e.g. Cairns 1989; Gaston et al. 2008). In accordance with Ashmole's theory, larger colonies have larger foraging ranges (Lewis et al. 2001) because of food depletion within the immediate vicinity of the colony (Ashmole 1963). Recent studies found that foraging sites of individuals from neighbouring colonies were spatially segregated to minimize intraspecific competition for the same resources (e.g. Grémillet et al. 2004; Wakefield et al. 2013). Seabird conspecifics from different breeding colonies may thus either occupy different foraging spaces and/or foraging niches, especially given that prey distribution may also vary around different colonies.

Foraging-niche width may be derived from the variation of isotopic values ("isotopic-niche width" proposed by Newsome et al. (2007); i.e., area spanned by isotopic values as coordinates) calculated from stable isotope analyses (SIA) of carbon and nitrogen. SIA is a common tool for integrating trophic information from different tissues over different time periods (Bearhop et al. 2004), and can be used to quantify foraging strategies at both the individual and population levels (Newsome et al. 2007).

Several studies have dealt with the short- and long-term consistencies of the variation of isotopic values at the individual level (e.g. Woo et al. 2008; Ceia et al. 2014a). However, existing isotopic studies at the colony level have often been based on visual observations. The possibility of tracking individuals from the corresponding colonies has often been dismissed because of technical constraints (e.g. Forero et al. 2002), or studies have focused on interspecific seabird communities (e.g. Harding et al. 2013; Bodey et al. 2014b).

GPS data loggers currently provide a common tool for analysing the year-round foraging behaviour of seabirds (e.g. Shamoun-Baranes et al. 2012). However, the sample size of tracking studies (of the same species at different breeding sites) is often small, and many studies have therefore focused on individual foraging patterns, instead of considering a multi-colony approach. Wakefield et al. (2013) reported that the colony-specific home ranges of tracked northern gannets (*Morus bassanus*) were strongly related to density-dependent, intraspecific competition. Gannets feed largely on pelagic shoaling fish and thus exclusively use the marine habitat for foraging. In contrast, we investigated the foraging behaviours of the omnivorous lesser black-backed gull (LBBG; *Larus fuscus*), which is a common opportunistic seabird species that utilises a broad range of foraging habitats both at sea and on land (e.g. Kubetzki and Garthe 2003).

We conducted a multi-year tracking study at six different breeding colonies in the southern North Sea, and examined colony-specific foraging areas by combining distributional patterns with conventional and isotopic dietary data from tracked individuals. All breeding colonies were located on islands with direct access to the open sea. Given that colony size and location are known to affect the foraging behaviour of seabirds, we expected differences in foraging behaviours in relation to the size of the colony and its location, in terms of distance from the mainland. According to foraging theory, we hypothesized that there would be clearly segregated foraging patterns with little spatial overlap among colonies, despite the close proximity of some colonies to each other. We anticipated similar, but less distinct, results for dietary segregation, given that individual diet preferences may vary. We also determined if foraging-habitat type (sea or land) affected the foraging behaviours of LBBGs from different colonies. We predicted that resource limitation within the immediate vicinity of the breeding colonies and avoidance of density-dependent competition might favour the use of marine and terrestrial habitats to different extents.

Materials and methods

Fieldwork

A total of 103 incubating LBBGs were caught at six German breeding colonies from 2008 to 2013 (Table 2, Fig. 2): the East and North Frisian Wadden Sea islands Borkum (BO), Juist (JU), Norderney (NO), Spiekeroog (SP) and Amrum (AM), and the offshore island of Helgoland (HE) (Table 1). All gulls were caught using walk-in traps placed above their nests. The gulls were recaptured after approximately 16 days to remove the GPS devices.

GPS telemetry

Streamlined GPS data loggers (Earth and Ocean Technologies, Kiel, Germany; Catnip Technologies, Hong Kong, China) were attached to the base of the four innermost tail feathers using TESA tape (Beiersdorf AG GmbH, Hamburg, Germany). The total weights of the two types of attached devices were 26 g and 30 g, respectively, which were 3.3% (range: 2.6–4.3%) and 3.6% (range: 3.0–4.3%) of the average body mass of most equipped LBBGs (mean ± SD: 797.4 ± 100.1 g; range: 609–976 g; $n_{birds} = 58$). The recording intervals of the devices were set to 2 min, except in individuals caught at SP in 2010, which were tracked every 3 min. Eight devices applied at JU and NO had a special schedule with a main recording interval of 5 min.

Instrumentation effect

Total weights of attached devices slightly exceeded the commonly used ‘3% limit’ (e.g. Kenward 2001; Phillips et al. 2003; Barron et al. 2010; but see Vandenabeele et al. 2012; Ludynia et al. 2012), and thus we conducted additional observations to exclude any effects of the devices on the gulls. We compared body masses at capture and recapture. We also monitored all clutches periodically. It was not possible to conduct detailed behavioural observations of unequipped birds, and we therefore monitored the behaviours of all caught individuals after release and during the following days of the fieldwork period instead. The maximum time that an activated trap was left on the nest was 45 min, depending on the weather conditions.

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Table 1 Study sites and periods of tagged *Larus fuscus*

Colony	Coordinates	Area (km²)	Number of breeding pairs (status)	Study period	Distance to mainland (km)
AM	54°41’N, 8°20’E	20.46	ca. 10,000[a] (2012)	13–31 May 2011 19 May–4 June 2012	24
BO	53°43’N, 7°18’E	30.74	ca. 1,500[b] (2012)	20 May–4 June 2012	17
HE	54°11’N, 7°53’E	1.70	ca. 600[c] (2013)	24 May–3 June 2008 2 May–3 June 2009 18–30 May 2010 17–28 May 2011	45
JU	53°40’N, 7°04’E	16.43	ca. 1,000[b] (2012)	16 May–4 Jun 2013	10
NO	53°43’N, 7°18’E	26.29	ca. 4,000[b] (2012)	16 May–3 June 2013	4
SP	53°46’N, 7°42’E	18.25	ca. 8,000[b] (2012)	14–23 May 2009 16 May–3 June 2010 19 May–5 June 2012	7

	AM-BO	AM-HE	AM-JU	AM-NO	AM-SP	BO-HE	BO-JU	BO-NO	BO-SP	HE-JU	HE-NO	HE-SP	JU-NO	JU-SP	NO-SP
Beeline distance (km)	162	63	140	129	112	100	20	40	69	80	65	47	18	47	18

[a]Verein Jordsand e.V. (unpubl. data); [b]Wadden Sea National Park Administration of Lower Saxony (unpubl. data); [c]Island Station of the Institute of Avian Research “Vogelwarte Helgoland” (unpubl. data). Numbers of breeding pairs are overall numbers for the corresponding islands

Foraging behaviour and utilization distribution

Any complete trip made by a gull that was clearly heading out of the relevant breeding colony, where the first and last positions were at the colony, was defined as foraging trip. The current study focused on the properties of the foraging trips and we therefore ignored all data during nest attendance and resting within or near the colony. The area close to the breeding colony is frequently used for preening or bathing, and trips for these purposes were assumed to be mostly within a distance of <2 km from the breeding colony, and were characterized by few movements and low instantaneous speeds. These trips were excluded from further analyses. The foraging-trip characteristics recorded included trip duration and total distance flown, and were calculated using the trip package 1.1.18 of R 3.1.1 (R Development Core Team 2014). Each GPS position was assigned visually to either land (i.e., mainland or islands) or sea (ArcGIS 10.0, ESRI 2011), and defined as the proportion of time flying over land for each trip, indicating a visit to either marine (“0”) or terrestrial (“1”) habitats.

Utilization distributions (UD) of the tagged animals were identified for each trip using the biased random bridge approach (BRB; Benhamou 2011; R package adehabitatHR 0.4.11; ‘BRB’ function: grid = 500, radius = 300, h_{min} = 100), taking into account the time dependence between relocations. BRB assumes that animals move following biased random walks, and supposes a drift between successive relocations. Individual intensity distribution (ID) and recursion distribution (RD) were also calculated accounting for areas in which the individuals stayed for a long time (ID) and frequently-visited areas (RD). Both measurements characterized profitable foraging areas that were exploited intensively, either through increasing residence time or more visits (Benhamou and Riotte-Lambert 2012). We calculated the areas (km²) of 50% and 95% UD, and 30% ID and RD and the corresponding utilization distribution overlap indices (UDOI, Fieberg and Kochanny 2005) between and within colonies using the same R package.

Identification of active foraging

Locations of active foraging were identified based on the calculated ID areas. All 30% ID areas were overlaid with the individual trip locations. Locations at the relevant colony islands as well as locations within 2 km from the breeding colony were excluded from this consideration. We identified locations of active foraging visually and could confirm an adequate match with the calculated 30% ID areas. We then selected all locations intersecting with the 30% ID areas as locations of active foraging. We summarised the characteristics of these active-foraging locations per trip and calculated the maximum beeline distance to the breeding colony, the proportion of locations at land/sea (referred to as proportion of foraging at land) and the proportion of locations during the day/night (referred to as proportion of foraging during the day), according to the trip properties noted above.

Dietary analyses

The prey compositions were compared among the breeding colonies by combined analyses of pellets from the entire colony and SIA of the tagged individuals. Pellets were collected randomly at each study site during the relevant study period and analysed to the lowest possible taxon according to Kubetzki and Garthe (2003). Only fresh pellets were collected, representing the gulls' diet over the preceding 2–3 days. We compared dietary diversities among colonies using a modification of the Shannon-Index (Shannon and Weaver 1949)

$$\mathrm{H}' = -\sum_{\mathrm{i}} p_i * \ln(p_i)$$

where H′ is the diversity and p_i is the relative frequency of each dietary component in all pellets per colony.

Carbon and nitrogen SIA is widely used for analysing the trophic ecology of seabirds (e.g. Inger and Bearhop 2008; Ceia et al. 2014b). δ^{13}C represents the foraging habitat, with decreasing ratios indicating more terrestrial feeding, while δ^{15}N reflects the consumer's trophic level (Inger and Bearhop 2008). Both parameters represent the gulls' diet over the last 3 days (plasma) to 3 weeks (red blood cells, RBCs), depending on the tissue analysed (Hobson and Clark 1993). We used RBCs in the current analysis because this represented the diet during the active logger periods. Blood samples (max. 0.5 ml corresponding to 0.75% of

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the total blood volume of the captured gulls; gauge needle: 0.40 × 20 mm) were taken during recapture from the cutaneous ulnar or brachial vein of most tracked individuals (n = 49), except for birds from HE, SP (2009), and one individual from JU. Most important prey items identified from former pellet analyses of LBBGs (e.g. Kubetzki and Garthe 2003; Schwemmer and Garthe 2005) were classified into six groups of prey items: “naturally captured fish” (*Clupea harengus*, *Sprattus sprattus*, *Callionymus lyra*), “discarded fish” (*Limanda limanda, Solea solea, Pleuronectes platessa, Gadus morhua, Merlangius merlangus, Eutrigla gurnardus, Trachurus trachurus, Belone belone*), “swimming crabs” (*Liocarcinus holsatus*), “mammals” (*Microtus arvalis, Arvicola terrestris, Talpa europaea*), “insects” (Staphilinidae sp., Carabidae sp.), “Earthworms” (*Lumbricus* sp.). Marine prey items were caught during multi-year research vessel surveys of the Institute for Hydrobiology and Fishery Science (University of Hamburg/Germany) and the Institute of Sea Fisheries (Thünen Institute, Hamburg/Germany). Terrestrial prey items were collected from regurgitates during capture or recapture, or caught at areas similar to the terrestrial habitats the gulls used.

RBC samples and prey items were freeze-dried and homogenised. SIA of RBCs and prey items was conducted at the Leibniz Institute for Zoo and Wildlife Research, Berlin, Germany. Stable carbon and nitrogen isotope values of blood samples were measured simultaneously via continuous-flow isotope ratio mass spectrometry using a Flash Elemental Analyzer linked to a Delta V Advantage Isotope Ratio Mass Spectrometer (both Thermo Finnigan, Bremen, Germany). Two laboratory standards were analysed for every 10 unknown samples, allowing instrumental drift over a typical 14 h run to be corrected. Stable isotope ratios were expressed in δ notation as ‰ based on the international standards V-Pee-Dee Belemnite (carbon) and AIR (nitrogen), according to $\delta X = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1{,}000$ where X is ^{15}N or ^{13}C and R is the corresponding ratio ^{15}N/^{14}N or ^{13}C/^{12}C. Based on internal standards (n = 165, tyrosin; Roth, Germany), the standard deviations were 0.16‰ and 0.29‰ for δ^{15}N and δ^{13}C, respectively.

We used trophic enrichment factors (TEFs) (+2.75 for $\delta\ ^{15}$N and −0.06 for $\delta\ ^{13}$C) (Steenweg et al. 2011) calculated for herring gulls (*L. argentatus*) and great black-backed gulls (*L. marinus*), because species-specific TEFs for LBBGs were not available. However, both *Larus* species have similar foraging and feeding ecologies to LBBGs (e.g. Cramp and Simmons 1983), suggesting that their TEF values were comparable.

Statistical analyses

All statistical analyses were carried out using R 3.1.1. Linear Mixed Models (LMM; Faraway 2006) based on the REML estimation were conducted (R package lme4 1.1-6). Multi-colony comparisons of trip characteristics included trip duration, total distance flown, areas of 95% and 50% UD, and 30% ID and RD, including the relevant intra-colonial overlaps as response variables in single models. Analyses of active foraging considered maximum distance to the relevant breeding colony and the proportions of active foraging at land/sea and during the day/night (day: 05:00–21:59 CEST; night: 22:00–04:59 CEST).

In mixed models, bird id was used as random factor to avoid pseudo replication. We conducted random effect models with ‘colony’ as a further random factor to make robust assumptions at the population level and to correct for multiple testing (Gelman, Hill and Yajima 2012). We also tested the effects of colony distance from the mainland, colony size, and the interaction of the two proportion variables (fixed effects) on the above response variables in separate LMMs with both random factors. These interactions had no significant effect on either parameter and were thus excluded from the models. We had only one measurement per bird for UD, ID and RD areas including the relevant intra-colonial overlaps, and these responses were therefore analysed without bird id as random factor. Study year had no influence on any response variable and was therefore excluded from further analyses. Sex (analysed following Suh et al. (2011)) was not considered in this study, to maximize sample size (available samples $n_{\mathrm{birds}} = 50$, no data from HE) and because the sex ratio was similar in all colonies (Generalized Linear Model, all $P > 0.15$). Body mass had no effect on any foraging parameter (LM, $F_{5,49} = 2.3$, $P = 0.1$, $n_{birds} = 58$).

To analyse the possibility that any effects of the four predictor variables on the respective response variables were caused by the inclusion of HE, which might be an outlier as the most remote breeding colony (Table 1; Fig. 2), we repeated all models excluding HE. The results changed in most parameters (compare Tables 2, 4, 5, 6): Trip duration and ID areas were unaffected by colony size, maximum distance to nest (i.e. foraging range), the proportion of active foraging at land and the RD areas were unaffected by the colony distance from the mainland, the UD areas and the intra-colonial overlap indices were unaffected by colony size and distance from the mainland, and the intra-colonial overlap indices were unaffected by colony when Helgoland was excluded. The effects of colony size and the proportion of time spent flying over land and during the day on these parameters remained the same, except for areas of 50% UD and the overlap indices of RD areas. Excluding HE would mean losing 19 birds and one level of the random factor colony. The latter can lead to a worse fit of the models just because of the exclusion of this colony, as e.g. Gelman and Hill (2006) recommend at least five levels for random factors for adequate model estimation. We thus decided to leave HE in the analyses and to represent all results including and excluding HE to enable comparison.

To provide a better comparison of effect sizes, the distance of each colony from the mainland and colony size were z-transformed using the ‘scale’ function. Model prediction and credible interval (CrI) were estimated by simulating the posterior distributions (R package arm 1.7-03) with 5000 simulations (Korner-Nievergelt et al. 2015). To assume normality, proportions were arcsine-transformed, maximum distance to nest, trip duration, total distance flown were log-transformed, and areas of 95% and 50% UD, 30% ID and RD were square-root-transformed. A Gaussian error distribution was used for all models. Visual inspection of residual plots found no obvious deviations of residual variances from homoscedasticity. Residuals were independent and identically distributed (in models excluding and including HE) (Korner-Nievergelt et al. 2015).

We compared isotopic ratios among colonies using Stable Isotope Bayesian Ellipses in R (SIBER), according to Jackson et al. (2011). We calculated the standard ellipse areas (SEAs) with correction for small sample sizes (SEAc, containing 40% of the data), the Bayesian estimate SEAb (number of posterior draws to make: 10,000) and the corresponding convex hull areas (TAs) according to Layman et al. (2007) following Jackson et al. (2011), using the package siar 4.2 (R package siar 4.2). LMs were performed to test for dependence of stable isotope values on colony size, colony distance from the mainland and body mass.

Sample size

Eighty-two out of 103 equipped LBBGs were successfully recaptured. Eighteen birds could not be recaptured, one lost its device, and two devices malfunctioned and failed to record any data. After the exclusion of incomplete trips and trips within < 2 km of the breeding colony, a total of 838 trips conducted by 79 birds were used to analyse trip properties. The 30% ID and RD areas, and active foraging were analysed for 824 trips by 78 birds, because the 30% ID and RD area calculation failed in one individual from AM. The parameters of active foraging (maximum distance from the nest, proportions of active foraging at land and during the day) were analysed for 811 trips by 78 birds.

Results

Instrumentation effect

Comparisons of the body masses of the equipped gulls at capture (mean ± SD: 818.3 ± 88.2 g, $n_{birds} = 58$) and recapture (784.2 ± 82.2 g) indicated an average body mass loss of 34.1 g (4.2%), which was not significant (Kruskal Wallis test, $\chi^2 = 2.2$, df = 1, $p = 0.1$, $n_{birds} = 58$). Thirty-eight individuals lost (range: 0.1–24.1%) and 17 gained body mass (range: 0.5–12.2%). Sixteen of the 103 equipped gulls (15.5%) lost their clutches as a result of predation, and two individuals refused to be captured while their clutch was covered with the trap. We confirmed chick hatching in the remaining individuals. The captured birds initially left the colony, but most returned after 5–10 min to continue incubating. No abnormal behaviour was detected during observations of the equipped individuals throughout the capture period. Several equipped birds ($n_{birds} = 34$) were later identified during migration by reading their colour bands at their wintering grounds (multiple sightings at different locations in England, France, Spain, Portugal and Morocco) and/or at the breeding colonies in subsequent years. One individual from SP was equipped twice in two subsequent years with no evidence of abnormal behaviour. We therefore considered the effects of the GPS devices on the gulls to be low, though behavioural and energetic effects could not completely be excluded.

Flight and foraging patterns

Foraging trips of LBBGs breeding at the colonies close to the coast targeted both land and sea. Birds from BO, JU, NO and SP flew in southerly or northerly directions, while AM birds flew mainly in north-easterly or north-westerly directions. The flight patterns of HE individuals were less directed, but spread around the island (Fig. 2). All colony-specific foraging trips were spatially segregated (Fig. 2).

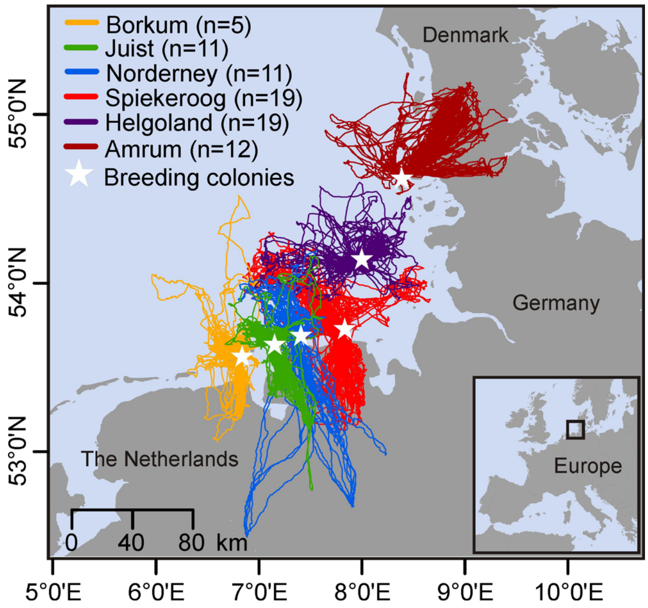

Fig. 2 Foraging trips of all tracked *Larus fuscus* (*n* = 79) in the southern North Sea. White stars represent the location of the breeding colonies. Different colours indicate birds from different breeding colonies

The trip durations of HE birds were shorter than those of birds from AM, BO and SP (Fig. 3). Similarly, individuals from AM and SP generally covered greater total distances than birds from BO, HE and JU (Table 2). Both parameters increased with increasing colony size, but were unaffected by the colony's distance from the mainland (Table 3). When excluding HE from the analyses, the effect of colony size on trip duration disappeared (Table 4), though the corresponding CrI was not far from zero. Trip duration decreased with the proportion of time spent flying during the day and increased with the proportion of time flying over land, indicating that trips were longer at night than during the day, and longer over land than over sea. However, the total distance flown was only marginally affected by the proportion of time flying over land (with a CrI very close to zero), and unaffected by the proportion of time flying during the day (Table 2).

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Table 2 Colony-specific foraging-trip parameters for *Larus fuscus* (n_{trips} = 838, n_{birds} = 79; areas of 30% ID and RD: n_{trips} = 811, n_{birds} = 78) derived from linear mixed models.

Colony	Statistical value	Trip duration (h)	Total distance travelled (km)	Maximum distance to nest (km)	Prop. of foraging at land	Prop. of foraging at day	95% UD area (km^2)	50% UD area (km^2)	30% ID area (km^2)	30% RD area (km^2)
AM (n = 13)	Mean	12.1	139.4	47.1	0.66	0.81	375.1	70.2	45.9	47.4
	SD	8.9	80.6	23.3	0.41	0.27	214.5	49.3	31.6	32.5
	Est. mean	7.9	96.0	33.2	0.69	0.88	304.5	55.8	34.3	37.6
	Lower CrI	5.2	61.8	20.8	0.21	0.78	214.5	38.8	23.7	25.2
	Upper CrI	12.0	151.2	53.6	0.99	0.95	410.5	75.6	47.1	51.6
BO (n = 6)	Mean	8.6	89.9	19.9	0.14	0.74	331.2	65.9	37.0	44.1
	SD	6.2	67.6	15.5	0.32	0.35	192.4	39.5	19.5	27.2
	Est. mean	6.5	65.5	16.3	0.09	0.86	272.8	52.3	29.5	35.7
	Lower CrI	4.2	42.1	10.2	0	0.76	167.7	32.3	17.8	21.9
	Upper CrI	10.0	104.3	26.5	0.51	0.94	396.3	77.3	44.7	52.4
HE (n = 19)	Mean	4.7	56.4	18.8	0.001	0.71	140.8	27.9	14.0	22.1
	SD	4.1	53.9	16.2	0.01	0.38	82.5	19.5	8.9	15.8
	Est. mean	3.9	44.9	15.4	0.002	0.83	151.4	29.6	15.0	23.0
	Lower CrI	2.7	30.9	10.0	0	0.74	99.1	19.4	9.5	15.4
	Upper CrI	5.7	66.6	23.7	0.24	0.91	212.6	41.9	21.7	32.4
JU (n = 11)	Mean	6.6	60.4	19.7	0.51	0.85	221.5	44.2	24.9	25.2
	SD	4.7	43.0	15.5	0.49	0.28	132.3	28.9	18.6	15.8
	Est. mean	5.4	51.7	15.1	0.49	0.91	214.7	41.9	22.5	26.3
	Lower CrI	3.7	35.8	9.8	0.11	0.84	139.3	26.9	14.0	16.5
	Upper CrI	7.8	74.9	23.2	0.88	0.96	303.8	60.0	33.0	38.6
NO (n = 11)	Mean	8.5	99.3	33.6	0.41	0.67	283.6	58.1	31.1	40.0
	SD	6.6	84.3	32.0	0.48	0.38	291.1	58.7	32.1	43.3
	Est. mean	6.5	68.7	21.6	0.41	0.81	219.2	44.0	23.1	30.7
	Lower CrI	3.9	39.5	11.6	0.002	0.68	141.1	29.0	14.3	20.2
	Upper CrI	10.9	120.8	40.2	0.95	0.91	312.4	62.7	33.3	43.5
SP (n = 19)	Mean	9.6	104.0	32.2	0.57	0.80	334.4	62.2	28.6	49.2
	SD	6.7	70.9	18.9	0.47	0.32	175.5	27.9	12.8	27.6
	Est. mean	7.1	80.6	26.9	0.59	0.89	293.3	55.2	26.2	41.4
	Lower CrI	6.0	66.4	21.7	0.44	0.84	219.5	41.1	18.8	31.0
	Upper CrI	8.5	97.8	33.3	0.74	0.93	374.6	71.5	34.9	53.4
Variance paremeters	Residual SD	0.77	0.75	0.74	0.55	0.47	4.45	2.59	1.99	2.21
	Lower CrI	0.74	0.71	0.71	0.52	0.44	4.25	2.24	1.72	1.90
	Upper CrI	0.81	0.79	0.78	0.58	0.49	4.67	3.05	2.33	2.60
	Between-colony SD	0.30	0.32	0.37	0.41	0.07	1.72	0.95	0.80	0.78
	Lower CrI	0.17	0.19	0.23	0.26	0.03	1.24	0.52	0.45	0.42
	Upper CrI	0.43	0.46	0.53	0.56	0.12	2.61	1.42	1.20	1.18
	Between-bird SD	0.33	0.39	0.44	0.33	0.13	X	X	X	X
	Lower CrI	0.29	0.34	0.40	0.29	0.11	X	X	X	X
	Upper CrI	0.38	0.44	0.50	0.36	0.15	X	X	X	X

Considerable differences between colonies are indicated if the 95% credible intervals (CrI) do not contain the estimated mean (est. mean) for the relevant colony.

Table 3 Comparison of effect sizes (est. mean) and symmetric 95% credible intervals (CrI) including the relevant variance parameters of foraging trip parameters for *Larus fuscus* (n_{trips} = 838, n_{birds} = 79; areas of 30% ID and RD: n_{trips} = 824, n_{birds} = 78) derived from linear mixed models

Predictor	**Statistical value**	**Trip duration (h)**	**Total distance travelled (km)**	**Maximum distance to nest (km)^a**	**Prop. of foraging during the day^a**	**95% UD area (km^2)**	**50% UD area (km^2)**	**30% ID area (km^2)**	**30% RD area (km^2)**
Colony size	Est. mean	0.15	0.26	0.23	-0.05	2.53	1.01	0.74	1.04
	Lower CrI	**0.05**	**0.14**	**0.11**	-0.13	**1.01**	**0.31**	**0.15**	**0.45**
	Upper CrI	**0.26**	**0.37**	**0.35**	0.02	**4.04**	**1.69**	**1.34**	**1.61**
Distance from the mainland	Est. mean	-0.08	-0.03	0.12	0.04	-1.73	-0.85	-0.43	-0.65
	Lower CrI	-0.17	-0.14	**0.01**	-0.03	**-3.31**	**-1.55**	-1.06	**-1.24**
	Upper CrI	0.02	0.08	**0.22**	0.11	**-0.20**	**-0.12**	0.20	**-0.06**
Prop. of foraging at land	Est. mean	0.24	0.17	0.85	0.45	-2.03	-3.20	-1.59	-3.36
	Lower CrI	**0.42**	**0.002**	**0.71**	**0.37**	**-2.99**	**-6.10**	-3.95	**-5.76**
	Upper CrI	**0.59**	**0.35**	**0.99**	**0.53**	**-1.10**	**-0.30**	0.77	**-0.98**
Prop. of foraging during the day	Est. mean	-0.46	0.09	-0.19	X	1.39	1.27	0.50	0.35
	Lower CrI	**-0.24**	-0.13	**-0.36**	X	-6.88	-2.54	-2.55	-2.79
	Upper CrI	**-0.02**	0.29	**-0.02**	X	9.57	5.07	3.60	3.47
	Intercept	1.78	4.02	2.86	0.10	17.43	7.22	5.25	6.95
	Lower CrI	1.60	3.84	2.69	-0.07	11.82	4.63	3.12	4.77
	Upper CrI	1.97	4.22	3.03	0.28	23.00	9.82	7.35	9.13
Variance parameters	Residual SD	0.76	0.75	0.74	0.51	5.50	2.54	1.97	2.11
	Lower CrI	0.73	0.71	0.70	0.48	4.72	2.18	1.70	1.81
	Upper CrI	0.80	0.78	0.78	0.53	6.50	3.01	2.34	2.52
	Between-colony SD	0.04	5.5e-08	n.a.	0.12	1.42	0.38	0.76	5.2e-08
	Lower CrI	0.02	2.4e-08	n.a.	0.19	2.38	0.17	0.36	2.2e-08
	Upper CrI	0.07	1.1e-07	n.a.	0.06	0.63	0.67	1.25	9.0e-08
	Between-bird SD	0.35	0.41	0.45	0.31	X	X	X	X
	Lower CrI	0.30	0.36	0.39	0.27	X	X	X	X
	Upper CrI	0.40	0.47	0.51	0.35	X	X	X	X

Predictors affected the single response variables if the CrI does not contain zero (bold). ^{a}parameters of active foraging: n_{trips} = 811, n_{birds} = 78

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Table 4 Comparison of effect sizes (est. mean) and symmetric 95% credible intervals (CrI) including the relevant variance parameters of foraging trip parameters for *Larus fuscus* (n_{trips} = 698, n_{birds} = 60; areas of 30% ID and RD: n_{trips} = 684, n_{birds} = 59) derived from LMMs excluding individuals from Helgoland.

Predictor	**Statistical value**	**Trip duration (h)**	**Total distance travelled (km)**	**Maximum distance to nest (km)**[a]	**Prop. of foraging at land**[a]	**Prop. of foraging at day**[a]	**95% UD area (km²)**	**50% UD area (km²)**	**30% ID area (km²)**	**30% RD area (km²)**
Colony size	Est. mean	0.10	0.21	0.25	0.17	-0.06	1.63	0.64	0.33	0.84
	Lower CrI	-0.02	**0.08**	**0.12**	**0.06**	-0.13	-0.17	-0.19	-0.35	**0.15**
	Upper CrI	0.22	**0.34**	**0.38**	**0.29**	0.01	3.51	1.47	1.00	**1.55**
Distance from the mainland	Est. mean	0.07	0.07	0.04	-0.10	0.07	1.50	0.49	1.18	0.10
	Lower CrI	-0.15	-0.16	-0.21	-0.31	-0.06	-2.16	-1.21	-0.19	-1.37
	Upper CrI	0.30	0.33	0.29	0.12	0.19	5.15	2.15	2.58	1.57
Prop. of foraging at land	Est. mean	0.59	0.36	0.89	X	0.45	-7.48	-3.28	-1.87	-3.31
	Lower CrI	**0.40**	**0.19**	**0.74**	X	**0.38**	**-14.88**	-6.69	-4.54	**-6.13**
	Upper CrI	**0.77**	**0.54**	**1.02**	X	**0.53**	**-0.15**	0.09	0.79	**-0.49**
Prop. of foraging at day	Est. mean	-0.41	-0.06	-0.28	0.89	X	-0.25	0.70	-0.35	-0.28
	Lower CrI	**-0.66**	-0.30	**-0.47**	**0.75**	X	-11.40	-4.32	-4.45	-4.64
	Upper CrI	**-0.16**	0.18	**-0.10**	**1.02**	X	10.84	5.76	3.71	4.07
	Intercept	1.91	4.11	2.83	-0.001	1.03	21.23	8.62	7.13	7.92
	Lower CrI	1.68	3.87	2.61	-0.18	0.04	13.22	4.85	4.18	4.67
	Upper CrI	2.14	4.34	3.04	0.18	1.11	29.43	12.44	10.14	11.21
Variance parameters	Residual SD	0.74	0.71	0.74	0.54	0.40	6.01	2.71	2.14	2.29
	Lower CrI	0.71	0.68	0.71	0.51	0.38	5.03	2.27	1.79	1.91
	Upper CrI	0.79	0.75	0.78	0.57	0.43	7.34	3.33	2.62	2.82
	Between-colony SD	0.07	0.05	n.a.	0.14	0.08	n.a.	n.a.	n.a.	n.a.
	Lower CrI	0.03	0.02	n.a.	0.07	0.03	n.a.	n.a.	n.a.	n.a.
	Upper CrI	0.13	0.10	n.a.	0.23	0.14	n.a.	n.a.	n.a.	n.a.
	Between-bird SD	0.34	0.39	0.45	0.35	0.15	X	X	X	X
	Lower CrI	0.29	0.33	0.39	0.30	0.12	X	X	X	X
	Upper CrI	0.39	0.45	0.51	0.40	0.17	X	X	X	X

n.a. = not assessable (i.e., SDs are so small that the model cannot estimate it properly). Predictors affected the single response variables if the CrI does not contain zero (bold). Results for UDOIs are shown in Online Resource 4). [a]parameters of active foraging: n_{trips} = 681, n_{birds} = 59

During active foraging, the maximum distance from the nest was longer in birds from AM and SP compared with birds from the other colonies (Table 2). Foraging locations were further from the relevant colony with increasing colony size (Table 3). Distance from the mainland was only slightly relevant in these birds (Table 3), and when excluding HE from the analysis its effect disappeared (Table 4). Birds also foraged further from their breeding colony at land than at sea (Table 3). Several individuals from JU and NO regularly foraged at landfill sites and a meat factory in Lower Saxony, about 135 km from both breeding colonies.

Foraging during the day was done closer to the breeding colony (Table 3). The proportion of foraging at land increased with increasing colony size (Fig. 4a), and decreased with increasing distance to mainland (Fig. 4b). However, the latter pattern did not apply when HE was excluded (Table 4). Foraging at land was mostly done during the day (Fig. 4c). Foraging during the day was unaffected by colony size and distance from the mainland (Table 3).

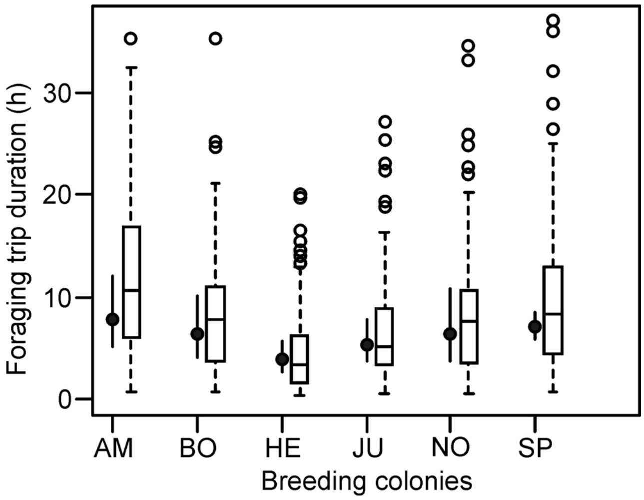

Fig. 3 Inter-colony comparison of foraging trip duration of all tracked *Larus fuscus* (*n* = 79) among different breeding colonies in the southern North Sea. White boxes represent 50% of the data between the first (25%) and third (75%) quartile. Upper and lower whiskers represent 25% of the remaining data. The median is represented by the horizontal black line. Black dots represent the estimated means resulting from LMMs including the symmetric 95% credible interval (CrI).

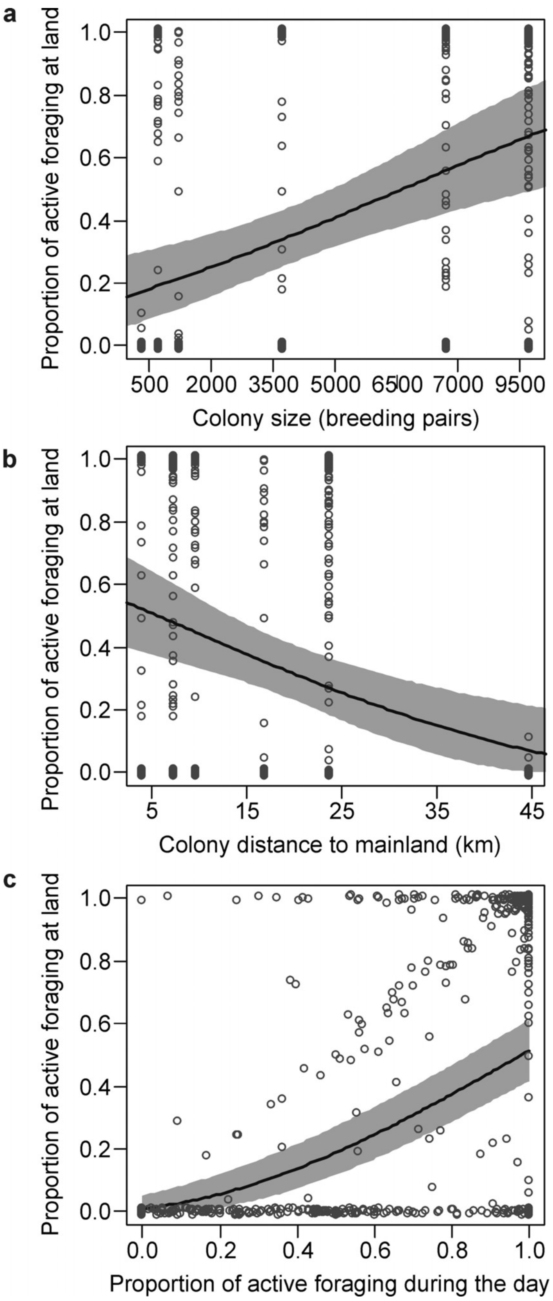

Fig. 4 Proportion of active foraging at land/sea in relation to **a** colony size (estimated mean (95% CrI), 0.21 (0.07–0.36)); **b** distance of colony from the mainland (-0.18 (-0.33– -0.03)); and **c** proportion of active foraging during the day/night (0.70 (0.58–0.80)) of all tracked *Larus fuscus* (*n* = 79). Residual SD was 0.50 (0.48–0.53), between-colony SD was 0.12 (0.06–0.19), and between-bird was SD 0.31 (0.27–0.35). Circles represent raw data, bold line represents predicted value for the population, and the symmetric 95% CrI is given in grey.

Utilization distribution

LBBGs from AM showed the largest UD and ID areas. Birds from SP used the largest RD area (Table 2), while individuals from HE used the smallest UD, ID and RD areas (Table 2). UD, ID and RD areas increased with increasing colony size (Table 3). This correlation disappeared for UD and ID areas, when HE was excluded from the analyses (Table 4). UD and RD areas decreased with the increasing colony distance to the mainland (though unaffected excluding HE; Table 4), and the proportion of time spent flying at land. Areas used for flying were thus smaller when LBBGs flew over land. However, areas used for foraging (ID areas) were similar when flying over land or sea, and independent of the colony location (Table 3). All area sizes were unaffected by the proportion of time spent flying during the day (Table 3). Simultaneously, all intra-colonial overlap indices were unaffected by colony size and distance to the mainland, though the effect sizes of the overlap indices were very low (Tables 5). However, both predictors affected the overlap indices, when HE was excluded (Table 6). The corresponding low effect sizes indicate a marginal meaning of colony size and distance to the mainland for the intra-colonial overlap. The overlap indices were similar when flying over land or sea, but increased when flying during the day (Tables 5, 6).

Table 5 Intra-colonial comparison of est. means and symmetric 95% CrI of UDOIs and isotopic ratios (RBC) of *Larus fuscus* (n = 79; isotopic ratios: n = 49) derived from LMMs.

Predictor	**Statistical values**	**Intra-colonial UDOI of 95% UD**	**Intra-colonial UDOI of 50% UD**	**Intra-colonial UDOI of 30% ID**	**Intra-colonial UDOI of 30% RD**	**δ^{13}C (‰)**	**δ^{15}N (‰)**
Colony size	Est. mean	-0.04	-0.02	-0.003	-0.010	-0.09	-0.22
	Lower CrI	-014	-0.04	-0.006	-0.030	-0.55	-0.70
	Upper CrI	0.06	0.01	0.001	0.010	0.37	0.25
Distance to mainland	Est. mean	-0.02	-0.004	-0.002	-0.008	-0.28	-0.34
	Lower CrI	-0.14	-0.04	-0.005	-0.031	-0.73	-0.82
	Upper CrI	0.10	0.03	0.002	0.015	0.17	0.13
Prop. of foraging at day	Est. mean	0.06	0.04	0.018	0.033	2.80	3.70
	Lower CrI	-0.13	-0.03	-0.012	-0.026	-0.16	**0.49**
	Upper CrI	0.26	0.12	0.048	0.095	5.69	**6.80**
Prop. of foraging at land	Est. mean	0.08	0.03	0.009	0.032	-7.47	-7.73
	Lower CrI	-0.003	-0.004	-0.004	**0.005**	**-9.48**	**-9.85**
	Upper CrI	0.17	0.06	0.023	**0.059**	**-5.42**	**-5.50**
	Intercept	0.14	0.03	-0.004	0.016	-18.98	15.43
	Lower CrI	-0.04	-0.04	-0.025	-0.036	-20.80	13.41
	Upper CrI	0.31	0.09	0.019	0.066	-17.11	17.42
Variance parameters	Residual SD	0.15	0.057	0.027	0.047	1.37	1.48
	Lower CrI	0.14	0.054	0.026	0.045	1.12	1.21
	Upper CrI	0.16	0.061	0.029	0.050	1.71	1.85
	Between-colony SD	0.11	0.05	0.007	0.033	n.a.	n.a.
	Lower CrI	0.08	0.03	0.004	0.022	n.a.	n.a.
	Upper CrI	0.17	0.07	0.012	0.051	n.a.	n.a.

The intra-colonial UDOIs of 30% ID and RD were analysed for 78 birds, because ID calculation failed for one individual from Amrum. NA = not available, n.a. = not assessable (i.e., SDs are so small that the model cannot estimate it properly). Predictors affect the single response variables decisively, if CrI do not contain zero (bold)

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Table 6 Intra-colonial comparison of est. means and symmetric 95% CrI of UDOIs of *Larus fuscus* (*n* = 60) derived from LMMs excluding the breeding colony Helgoland

Predictor	**Statistical values**	**Intra-colonial UDOI of 95% UD**	**Intra-colonial UDOI of 50% UD**	**Intra-colonial UDOI of 30% ID**	**Intra-colonial UDOI of 30% RD**
Colony size	Est. mean	-0.06	-0.02	-0.004	-0.016
	Lower CrI	**-0.09**	**-0.04**	**-0.007**	**-0.025**
	Upper CrI	**-0.02**	**-0.01**	**-0.001**	**-0.006**
Distance to mainland	Est. mean	0.06	0.03	0.004	0.015
	Lower CrI	**0.02**	**0.01**	**0.001**	**0.005**
	Upper CrI	**0.09**	**0.04**	**0.006**	**0.025**
Prop. of foraging at day	Est. mean	0.10	0.03	0.017	0.043
	Lower CrI	-0.14	-0.05	-0.013	-0.032
	Upper CrI	0.34	0.12	0.048	0.118
Prop. of foraging at land	Est. mean	0.02	-0.002	-0.004	0.019
	Lower CrI	-0.07	-0.04	-0.018	-0.011
	Upper CrI	0.11	0.03	0.010	0.049
	Intercept	0.12	0.03	0.005	0.010
	Lower CrI	-0.05	-0.03	-0.019	-0.046
	Upper CrI	0.29	0.10	0.029	0.066
Variance parameters	Residual SD	0.15	0.054	0.025	0.050
	Lower CrI	0.14	0.051	0.023	0.046
	Upper CrI	0.16	0.059	0.026	0.053
	Between-colony SD	0.06	0.02	0.003	0.018
	Lower CrI	0.03	0.01	0.001	0.010
	Upper CrI	0.10	0.04	0.005	0.031

The intra-colonial UDOIs of 30% ID and RD were analysed for 59 birds, because ID calculation failed for one individual from Amrum. Predictors affect the single response variables decisively, if CrI do not contain zero (bold).

There was little overlap between the colony-specific UD, RD and ID values (Fig. 5a,b; Table 8), and the average overlap between all colonies was ≤0.01. The maximum overlap of all UD, ID and RD areas occurred between the adjacent colonies on JU and NO (Table 8), though the degree of overlap was not significantly related to the distance between the relevant colonies (one-way ANOVA, $F_{1,8} = 3.421$, adj. $R^2 = 0.212$, $P = 0.102$, $n = 10$). There was no overlap between AM individuals and any other colony investigated (Fig. 2, Fig. 5a,b). Intra-colonial overlaps of all utilization distribution areas were generally low (Tables 5, 7), but higher than the inter-colony overlaps (Table 8). The individual 30% ID areas particularly, showed only marginal overlap. These results suggest that individuals from the same colony used different areas for intensive foraging, rather than sharing them. The greatest intra-colonial overlap occurred in individuals from BO and JU (Table 5).

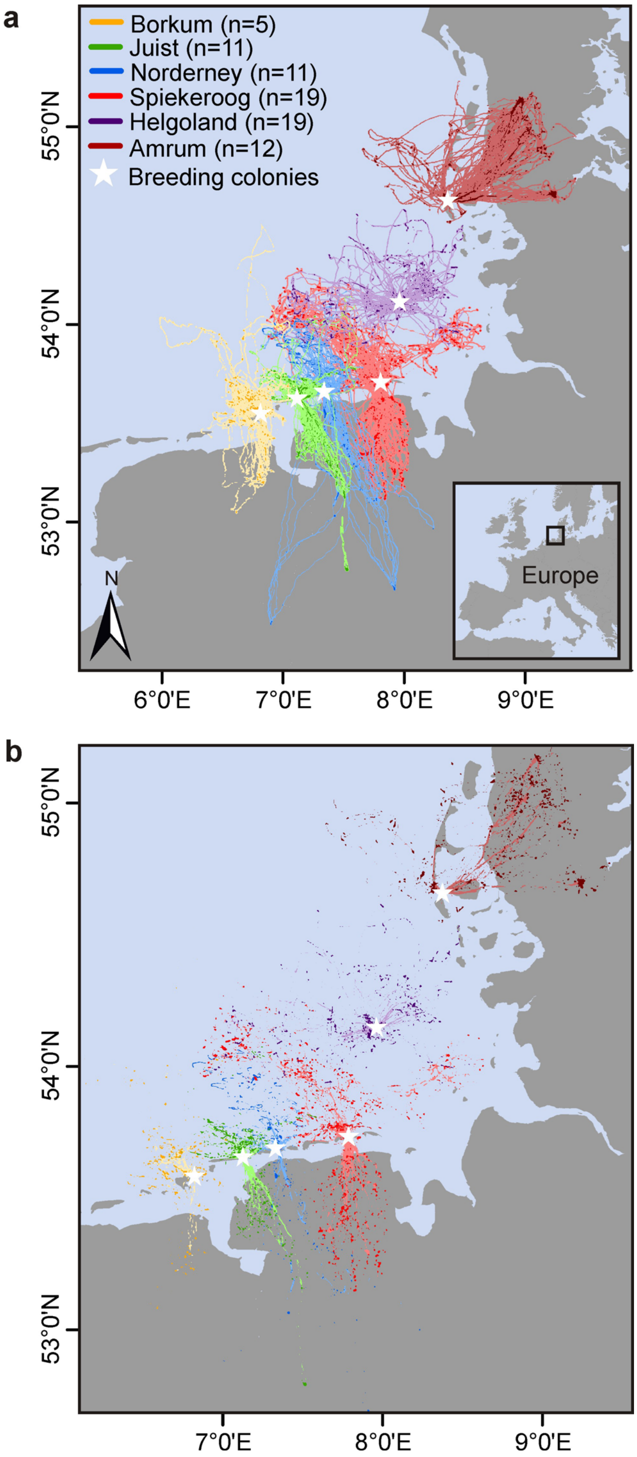

Fig. 5 **a** Areas of 95% (light-shaded colours) and 50% (dark-shaded colours) utilization distribution; and **b** areas of 30% recursion distribution (light-shaded colours) and intensity distribution (dark-shaded colours) of all tracked *Larus fuscus* (n = 78) in the southern North Sea. White stars represent the location of the breeding colonies. Different colours indicate birds from different breeding colonies

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Table 7 Colony-specific comparison of raw data means, standard deviations (SD) and estimated means (est. mean) including the 95% credible intervals (CrI) of intra-colonial UDOIs, and isotopic ratios (RBC) of *Larus fuscus* (*n* = 79; isotopic ratios: *n* = 49) derived from LMMs.

Colony	Statistical values	Intra-colonial UDOI of 95% UD	Intra-colonial UDOI of 50% UD	Intra-colonial UDOI of 30% ID	Intra-colonial UDOI of 30% RD	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)
AM	Mean	0.08	0.008	0.0005	0.006	-22.36	12.22
	SD	0.11	0.010	0.0006	0.006	1.17	1.26
	Est. mean	0.05	0.006	0.0003	0.004	-21.97	12.60
	Lower CrI	0.04	0.004	0.0001	0.002	-23.02	11.49
	Upper CrI	0.07	0.008	0.0006	0.005	-20.91	13.64
BO	Mean	0.17	0.026	0.0015	0.014	-18.91	16.33
	SD	0.08	0.010	0.0012	0.008	1.64	1.65
	Est. mean	0.14	0.022	0.0006	0.011	-19.81	15.52
	Lower CrI	0.09	0.015	0.0002	0.007	-21.21	14.03
	Upper CrI	0.20	0.030	0.0012	0.016	-18.43	17.05
HE	Mean	0.04	0.006	0.0012	0.003	NA	NA
	SD	0.16	0.032	0.0127	0.014	NA	NA
	Est. mean	0.02	0.002	0.0001	0.001	NA	NA
	Lower CrI	0.01	0.001	0.0001	0.0004	NA	NA
	Upper CrI	0.03	0.003	0.0002	0.001	NA	NA
JU	Mean	0.12	0.014	0.0009	0.012	-21.36	13.98
	SD	0.12	0.015	0.0010	0.016	2.41	2.50
	Est. mean	0.09	0.009	0.0005	0.007	-21.21	14.02
	Lower CrI	0.07	0.006	0.0002	0.004	-22.38	12.81
	Upper CrI	0.11	0.012	0.0008	0.009	-20.10	15.21
NO	Mean	0.02	0.002	0.0003	0.002	-20.36	14.23
	SD	0.03	0.003	0.0005	0.003	1.64	1.87
	Est. mean	0.02	0.002	0.0002	0.001	-20.51	14.21
	Lower CrI	0.01	0.001	0.00003	0.0004	-21.57	13.08
	Upper CrI	0.03	0.003	0.0004	0.002	-19.41	15.35
SP	Mean	0.06	0.006	0.0011	0.005	-20.87	14.38
	SD	0.16	0.029	0.0116	0.014	2.67	2.53
	Est. mean	0.04	0.003	0.0002	0.003	-20.87	14.33
	Lower CrI	0.03	0.002	0.0001	0.002	-21.96	13.15
	Upper CrI	0.05	0.004	0.0003	0.013	-19.84	15.46
Variance parameters	Residual SD	0.15	0.058	0.027	0.047	2.02	2.06
	Lower CrI	0.14	0.054	0.026	0.044	1.68	1.71
	Upper CrI	0.16	0.060	0.029	0.050	2.50	2.56
	Between-colony SD	0.10	0.04	0.006	0.029	0.94	1.16
	Lower CrI	0.07	0.03	0.003	0.022	0.45	0.62
	Upper CrI	0.12	0.05	0.009	0.037	1.49	1.78

Areas of 30% ID and RD were analysed for 78 birds, because calculation failed for one individual from Amrum (AM). Considerable differences between colonies are indicated, if colony-specific CrI do not overlap with each other.

Table 8 Inter-colonial utilization distribution overlap index (UDOI) of 95% and 50% utilization distribution (UD), 30% intensity distribution (ID) and recursion distribution (RD) of equipped *Larus fuscus*. Areas of individuals from Amrum (AM) did not overlap with those of any other colony and are therefore not shown

Colony	UDOI of 95 % UD				UDOI of 50 % UD				UDOI of 30 % ID				UDOI of 30 % RD			
	mean	SD	min	max	mean	SD	min	max	mean	SD	min	max	mean	SD	min	max
BO-HE	0.0003	0.0007	0	0.0016	0	0.0001	0	0.0006	0	0	0	0.0003	0	0	0	0.0002
BO-JU	0.0002	0.0005	0	0.0020	0	0	0	0	0	0	0	0	0	0	0	0.0001
BO-NO	0.0003	0.0004	0	0.0014	0	0	0	0	0	0	0	0	0	0	0	0
BO-SP	0.0001	0.0001	0	0.0007	0	0	0	0.0001	0	0	0	0	0	0	0	0
HE-JU	0.0002	0.0005	0	0.0055	0	0	0	0.0001	0	0	0	0	0	0	0	0.0001
HE-NO	0.0003	0.0006	0	0.0040	0	0	0	0	0	0	0	0	0	0	0	0.0001
HE-SP	0.0001	0.0005	0	0.0075	0	0	0	0.0002	0	0	0	0.0001	0	0	0	0.0001
JU-NO	0.0097	0.0390	0	0.3670	0.0009	0.0035	0	0.0268	0.0001	0.0002	0	0.0017	0.0005	0.0033	0	0.0340
JU-SP	0.0017	0.0027	0	0.0170	0	0	0	0.0003	0	0	0	0.0003	0	0	0	0.0004
NO-SP	0.0027	0.0044	0	0.0314	0.0002	0.0004	0	0.0040	0.0001	0	0	0.0009	0.0001	0.0001	0	0.0017

Dietary analyses

Pellet analyses demonstrated a varied dietary composition (Table 9). Swimming crabs (*Liocarcinus holsatus*) were the most abundant prey items in pellets from AM and BO, as well as HE pellets, where crabs and fish were almost the only dietary components. The proportion of terrestrial prey items increased in AM pellets between 2011 and 2012. Earthworms and insects were the main components in pellets from JU, NO and SP. Dietary diversity was lowest in HE (Table 9), though it did not differ significantly among the colonies or among years (Kruskal Wallis Test, $\chi^2 = 8$, df = 8, $P = 0.43$). Several kneecaps from pigs were found during pellet collections at NO and JU in 2013, associated with distant foraging at the visited meat factory.

Table 9 Dietary composition (%) and diversity (H') of prey items in pellets of *Larus fuscus*. "Others" represents birds, eggs, grain and seeds. The grey scale represents a gradient from small (white) to high values (dark grey)

Colony	Year	*n*	Bivalves	Bristleworms	Earthworms	Crabs	Insects	Fishes	Mammals	Waste	Others	H'
AM	2011	160	11.4	3.8	4.2	59.9	6.8	5.8	3.3	0.6	4.1	1.21
AM	2012	122	16.3	1.6	12.3	30.9	18.1	4.6	2.3	1.6	12.4	1.74
BO	2012	93	29.2	0	15.4	30.7	12.0	6.1	5.0	0	1.6	1.70
HE	2009	144	0.1	0.9	0	24.8	0	65.5	0.7	1.4	5.6	0.91
HE	2011	87	1.1	0.3	0	79	0.4	16.8	2.1	0.2	0	0.61
JU	2013	129	7.2	2.0	23.4	11.6	27.2	5.4	8.1	7.2	7.8	1.77
NO	2013	121	0.5	1.2	33.5	5.0	34.2	3.4	5.3	3.5	13.4	1.55
SP	2010	45	5.3	3.8	10.4	10.2	14.2	28.0	11.3	8.9	7.8	2.88
SP	2012	131	0.8	0	35.8	8.9	31.6	5.2	4.2	1.3	12.2	1.49

Overall, the results of SIBER analyses of stable carbon and nitrogen from RBC were in line with the pellet analyses: Most colonies showed variable isotopic signatures indicating both a broad range of marine and terrestrial prey items and the use of prey from low as well as high trophic levels. AM birds showed the smallest SEAc and JU birds the largest (Fig. 6a; Table 10). Pellet analysis of BO gave slightly different results than the SIA results for this colony. This could be due to the fact that herring gulls were breeding in a mixed colony with LBBG and some pellets might have been misallocated. Collected pellets thus might partly present the diet of both species, and have to be interpreted with caution.

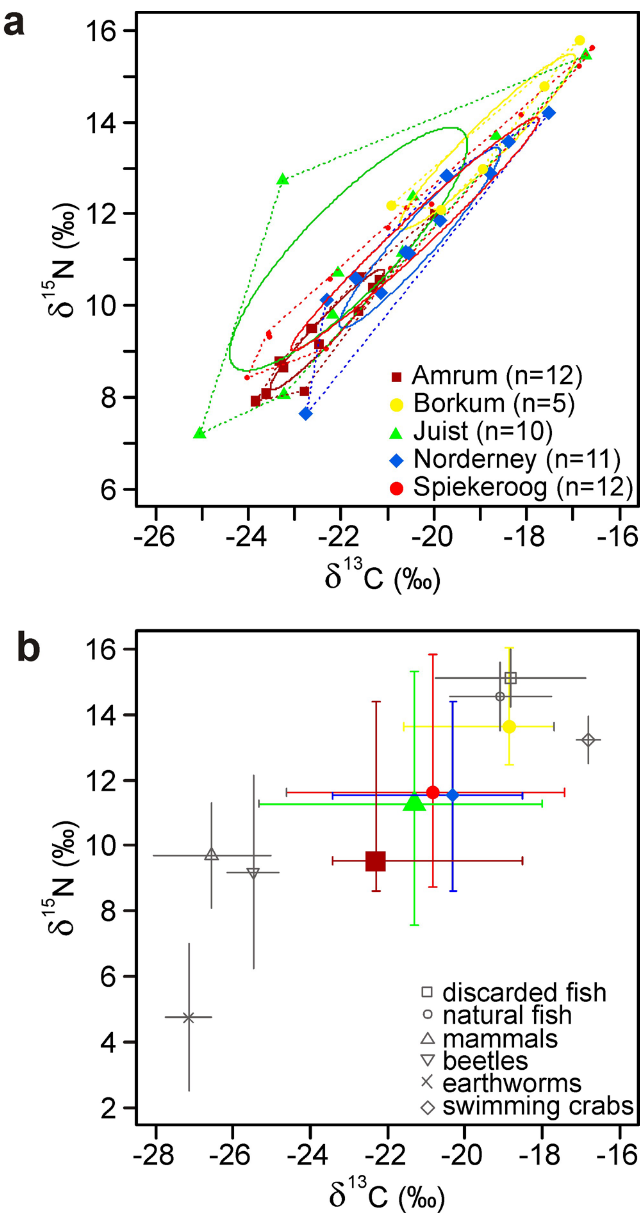

Fig. 6 a Standard ellipse areas corrected for small sample sizes (SEAc, 40% credible interval) following Jackson et al. (2011) based on stable isotope values (δ^{13}C and δ^{15}N) in red blood cells and **b** colony-specific isotopic values (mean ± SD) of *Larus fuscus* (*n* = 49) from different breeding colonies during the incubation periods from 2010 to 2013. Dotted lines indicate the layman metric of the convex hull area (TA). Different colours indicate different breeding colonies including all study years

Generally, more-marine diets had higher $\delta^{15}N$ values and thus were associated with feeding at higher trophic levels (Fig. 6a, b). Most SEAcs overlapped with each other (Fig. 6a; Table 10), except those of birds from BO and AM. BO individuals generally fed on more marine prey and consequently at a higher trophic level than AM individuals (Fig. 6b), while all other colonies showed similar means (Fig. 6b). However, $\delta^{13}C$ and $\delta^{15}N$ ratios were unaffected by colony size and distance from the mainland (Table 5).

The dietary composition and SEAcs derived from pellet analyses and SIBER differed slightly between years in repeatedly-sampled colonies (AM, HE, SP) (Tables 9, 10; Fig. 7).

Table 10 Colony-specific results of Stable Isotope Bayesian Ellipses In R (SIBER) of red blood cells from captured *Larus fuscus* (*n* = 49). Area of the standard ellipse corrected for small ample sizes (SEAc, 40% credible interval), the Bayesian approximation of the standard ellipse area (SEAb) and the layman metric of convex hull area (TA) according to Jackson et al. (2011).

	AM (*n* = 12)	BO (*n* = 5)	JU (*n* = 10)	NO (*n* = 11)	SP (*n* = 12)
SEAb	1.26	2.50	9.66	2.91	3.65
SEAc	1.38	3.33	10.87	3.23	4.01
TA	2.61	2.38	19.62	6.23	6.29

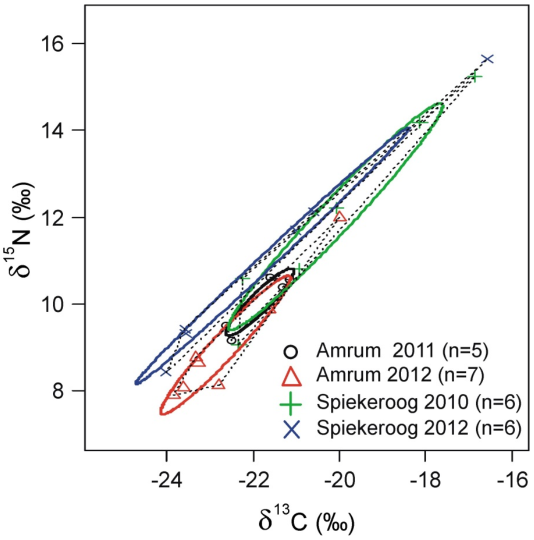

Fig. 7 Standard ellipse areas corrected for small sample sizes (SEAc, 40% CrI) following Jackson et al. (2011) based on stable isotope values ($\delta^{13}C$ and $\delta^{15}N$) in RBC of incubating *Larus fuscus* (*n* = 24) from the breeding colonies Amrum (AM) and Spiekeroog (SP) during incubation periods from 2010 to 2012. Ellipses represent the area of the standard ellipses (SEAc, 40 % CrI), the black dotted lines indicate the layman metric of convex hull area (TA). Different colours indicate different breeding colonies split between different years for multiple sampled colonies

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Discussion

We aimed to identify and explain the diverse foraging behaviours of LBBGs from different colonies by tracking foraging individuals from six breeding colonies of varying size located at different distances to the mainland. LBBGs showed colony-specific foraging behaviours in terms of spatially segregated flight and foraging patterns, which were influenced by colony size, foraging habitat (marine or terrestrial), and partly by the colony's distance from the mainland.

Spatial segregation and habitat use

LBBGs flew further and for longer and foraged further from their breeding colonies when colony size, and thus density-dependent competition, were large. Likewise, they increased their areas of UD and RD. These results are in accordance with Ashmole (1963). LBBGs increased their foraging range and used more-distant foraging areas in response to intraspecific competition, not only from neighbouring conspecifics but also from individuals in the same colony. The low inter-colonial overlap of ID further supports these findings and indicates the use of clearly-segregated foraging sites, according to Cairns (1989) and Wakefield et al. (2013), despite the closeness of the colonies to each other.

As expected, the intra-colony overlap was higher than the inter-colony overlap, but individuals from the same colony still showed segregated patterns, especially in terms of individual ID areas, indicating individual specialization in foraging sites. LBBGs thus not only avoid intraspecific competition from neighbouring colonies, but also from conspecifics within the same colony. This is in line with a recent study on Cory's shearwaters (*Calonectris borealis*) by Ceia et al. (2014a), who reported at least partial segregation between foraging trips of individuals from two adjacent sub-colonies. However, the effect sizes were close to zero, suggesting that these overlaps were largely independent of colony size, colony distance from the mainland, the visited habitat and the time of day.

Foraging patterns

Spatial segregation of LBBGs, primarily caused by density-dependent competition, was expressed not only by longer trips and further trips from the relevant breeding colony, but also by foraging in different habitats. Larger colony size was associated with a higher proportion of terrestrial foraging. As expected, individuals from coastal colonies tended to forage at land rather than at sea. In addition to avoiding intraspecific competition, the increase in terrestrial foraging might also reflect a continuously progressing food shortage at sea (Votier et al. 2004; Bertrand et al. 2012). Camphuysen et al. (2010) found an increase of consumption of mammalian prey by herring gulls (*L. argentatus*) and LBBGs, and predicted an increase in inland breeding for both species as a result of the apparent food shortage at sea. Following Bicknell et al. (2013), the amount of discards from fishing vessels, which represents an important food source for LBBGs (Camphuysen 1995; Garthe and Hüppop 1998), has also decreased in recent years, which could have an impact on the foraging behaviour, as well as the spatial distribution of scavenging seabirds (Votier et al. 2013; Bodey et al. 2014a). The effect of a lack of discards on LBBGs might also be reflected by the pellet analyses of HE individuals, which demonstrated a switch from mostly discarded fish in 2009 to predominantly swimming crabs in 2011, associated with a four-week strike of the German, Dutch and British shrimp fishermen during our study period in 2011.

Terrestrial foraging was mostly done during the day, while birds flew to sea at night. Because LBBGs hunt visually (Glutz von Blotzheim and Bauer 1982), foraging at night is only possible in illuminated places, e.g. behind fishing vessels (Garthe and Hüppop 1996).

Possible advantages of terrestrial foraging might include the relatively uniform distribution of prey such as insects and earthworms, depending on the habitat type (Palm et al. 2013; Hackenberger and Hackenberger 2014), which, together with their limited mobility, suggests that terrestrial prey might reduce the foraging efforts required by gulls. The uniform distribution of terrestrial prey means that there is little competition for this food source, compared with marine prey, which is unpredictably and patchily distributed (Weimerskirch 2007), apart from the case of discarded fish (Cama et al. 2012). Levels of intraspecific and interspecific competition during scavenging behind fishing vessels are high (Furness 1992; Garthe and Hüppop 1998) and require a certain assertiveness (Camphuysen 1995; Tasker et al. 2000).

Terrestrial foraging also presents challenges, however, because the gulls need to consume more prey items to meet their energy requirements. The nutrient contents of marine and terrestrial prey are similar (Golley 1961; Hislop et al. 1991; Finke 2002). Gulls generally performed longer trips and foraged further from their breeding colonies at land, which might be related to higher flight costs and energy requirements over land (but see Baudinette and Schmidt-Nielsen (1974) and Ellis (1984) for lower flight costs during gliding than during flapping). Increased flight costs could be compensated for by visiting already-known terrestrial foraging sites with good feeding conditions. The gulls could have used terrestrial habitats closer to the colony, assuming that food availability was similar to more distant areas, thus saving time and energy. However, they appeared to focus on predictable sites such as landfills and a meat factory about 135 km from the breeding colonies, as supported by the relatively straight and narrow routes flown to these inland areas. This could also explain the smaller UD, ID and RD areas at land compared with marine sites. LBBGs probably prefer to forage regularly at well-known sites that promise easily available prey with high nutritional value, such as the landfill sites and meat factory visited by birds from JU and NO. However, foraging at these sites might also be competitive, and further analysis of foraging-site utilisation on the individual level would help to clarify this issue. Detailed habitat mapping during the tracking period would help to clarify the reasons why LBBGs choose to fly long distances to terrestrial foraging sites. Whether or not the distribution of LBBGs during the breeding period is generally shifted towards terrestrial habitats remains unclear.

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Dietary segregation

Dietary analyses support the above findings. HE individuals preyed mainly on fish and swimming crabs, while birds from the more coastal colonies had a broad diet including marine and terrestrial components. Isotopic analyses identified BO as a mainly marine-feeding and AM as a markedly terrestrial-feeding colony. Isotopic ratios were also independent of colony size and distance from the mainland. This suggests that LBBGs use segregated foraging sites in different habitats, but that these sites showed similar prey availability within the two main foraging habitats (Ceia et al. 2014a). However, dietary segregation might occur at the individual, rather than the colony level, as shown e.g. for dolphin gulls (*Leucophaeus scoresbii)* by Masello et al. (2013).

In summary, LBBGs show colony-specific, spatially-segregated foraging patterns during incubation. Dietary segregation at the colony level is rare, suggesting that LBBGs forage in spatially-segregated sites, often in opposing habitats, but focus on similar prey within these habitats. The foraging differences help to avoid intraspecific competition and are related to colony size and/or distances from the mainland. Foraging behaviour is also affected by foraging habitat, given that trips were both temporally and spatially longer and UD areas were smaller at land than at sea. Inland foraging might thus also help to avoid density-dependent competition. In addition to colony-specific foraging patterns, individual specialization also occurs, demonstrating avoidance of competition at a very small scale. Given that birds are particularly constrained in terms of their foraging-trip duration and distance during the chick-rearing compared with the incubation phase, further studies are needed to analyse foraging strategies throughout the annual cycle.

Acknowledgements

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Ethics statement

All institutional and national guidelines for the handling and the equipment of birds were followed. Birds were caught, ringed and equipped under licenses issued by the National Park Administration of the Wadden Sea National Park of Lower Saxony, the Lower Saxony State Office for Consumer Protection and Food Safety (file number: 33.14-42502-04-11/0666), the State Agency for Agriculture, Environment and Rural Areas Schleswig-Holstein and the Ministry of Energy transition, Agriculture, Environment and Rural Areas Schleswig-Holstein, Germany (file numbers: V 312-72241.121-37 (34-4/11), V 312-7224.121-37 (80-6/13)). All animals were handled in strict accordance with good animal practice to minimize handling time and stress.

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CHAPTER II:
Individual factors influencing sexual segregation in foraging habitats in a marine top predator

Corman AM, Voigt CC, Garthe S (submitted) Individual factors influencing sexual segregation in foraging habitats in a marine top predator

Individual factors influencing sexual segregation in foraging habitats in a marine top predator

Anna-Marie Corman, Christian C. Voigt and Stefan Garthe

Abstract

Sex-specific foraging behaviour, including spatial segregation, occurs in several seabird species. Sexual segregation may be attributable to sexual size dimorphism, differences in parental investment, varying energetic demands, or individual specialisations. The last of these may cause complex confounding effects both within and between the sexes, resulting in evident differences in seabird foraging patterns. We studied sex-specific differences in the foraging behaviours of incubating lesser black-backed gulls (*Larus fuscus*) using GPS tracking and isotopic data, together with heterophil/leukocyte (H/L) ratios as a measure of persistent stress levels. We determined the effects of sex, body mass, and H/L ratio on gull foraging characteristics to account for within-sex differences. Males predominantly foraged at sea, while females tended to forage inland. Individual body mass and stress levels generally had opposite effects on sex-specific foraging characteristics, suggesting different strategies for coping with stress within and between the sexes. Sexual segregation in terms of foraging habitat in lesser black-backed gulls seems to be triggered by their slight male-biased sexual size dimorphism, linked to the avoidance of intraspecific competition, as well as to sex-specific nutrient requirements, probably in relation to differences in parental effort.

Keywords: GPS tracking, sex-specific foraging strategy, *Larus fuscus*, sexual size dimorphism, stable isotopes, white blood cell counts

Introduction

Sex-specific foraging behaviours have been demonstrated for a range of seabird species (Lewis et al. 2002; Catry et al. 2006) and are largely related to sexual size dimorphism, resource competition between the sexes, intra-sexual differences in parental care, and the different energetic demands of males and females (Lewis et al. 2002; Weimerskirch et al. 2009; Quintana et al. 2011; Ludynia et al. 2013). Sexual size dimorphism might lead to segregation in terms of use of different foraging sites (González-Solís et al. 2000; Quillfeldt et al. 2011; Cook et al. 2013; Ratcliffe et al. 2013), prey types and/or sizes (Bearhop et al. 2006; Quillfeldt et al. 2011), or times of day (Paredes et al. 2008). The smaller sex usually forages further from the colony involving more active foraging behaviours (González-Solís et al. 2000; Weimerskirch et al. 2006; Weimerskirch et al. 2009; Walter et al. 2014). The smaller sex may also be outcompeted by the larger, more competitive one and thus be forced to forage in lower-quality habitats, though this seems to vary according to the study site and species (González-Solís et al. 2000; Weimerskirch et al. 2009; Jaeger et al. 2014). However, sexual size dimorphism in turn may have evolved as a result of sexual selection, intraspecific competition for food resources, or different parental roles, and may thus be the result, as well as the cause of sexual segregation (Hedrick and Temeles 1989; Catry et al. 2006; Weimerskirch et al. 2009).

Between-sex differences in parental care and sex-specific energetic requirements are common in monomorphic seabird species (Phillips et al. 2011), while distinct foraging behaviours in size-dimorphic species tend to be related to their differences in body size. However, several studies have reported the importance of different energetic requirements for sexual segregation in species with distinct sexual size dimorphism (Lewis et al. 2002; Ludynia et al. 2013). In most cases, sexually-distinct foraging behaviours are determined by a complex combination of all these factors, and identifying the precise causes of sex-specific behaviours in a certain species remains difficult (Phillips et al. 2011; Ludynia et al. 2013).

Recent studies investigated sex-specific foraging behaviours in seabird species using isotopic ratios ($\delta^{13}C$ and $\delta^{15}N$) to demonstrate differences in prey composition and thus dietary segregation between the sexes (Phillips et al. 2011; Ludynia et al. 2013; Mancini et al. 2013). Stable-isotope analyses (SIA) of different tissues are commonly used to reveal dietary information relating to habitat type and trophic level (Bearhop et al. 2004; Inger and Bearhop 2008). The combination of this information with data on flight and foraging patterns derived from GPS tracking allows foraging strategies to be identified and quantified (Newsome et al. 2007; Phillips et al. 2011; Harding et al. 2013; Ceia et al. 2014b).

In addition to body size and mass, foraging performance may also be affected by individual fitness. During the breeding season, seabirds need to balance self-provisioning with nest defence, incubation, and chick-rearing. Breeding thus represents a demanding and stressful stage of the birds' annual cycle (Hanssen et al. 2005; Quillfeldt et al. 2008), and persistent stress may affect individual foraging behaviours. The leukocyte profile, especially the heterophil/lymphocyte (H/L) ratio, is commonly used as an indirect measure of persistent, physiological stress in birds (Davis et al. 2008; Müller et al. 2011). High H/L ratios may be related to susceptibility to infection (Al-Murrani et al. 2006) or survival to the subsequent breeding season (Lobato et al. 2005; Davis et al. 2008).

In this study, we tracked incubating lesser black-backed gulls (LBBGs) from different island colonies in the southern North Sea to determine the relationships between sex and foraging behaviours. LBBGs are surface-feeding generalists that feed mainly on marine and terrestrial prey items (Camphuysen 1995; Kubetzki and Garthe 2003; Camphuysen et al. 2010; Schwemmer et al. 2013). We accounted for body mass and H/L ratio and their possible associations with sex to exclude the possibility of sexual size dimorphism as the only factor responsible for sexually-distinct foraging strategies, and to allow assessment of the role of individual variations (Sommerfeld et al. 2013; Ratcliffe et al. 2013). We expected to find spatial segregation between the sexes (Catry et al. 2006; Phillips et al. 2011). We particularly predicted that the slightly larger and stronger males (Olsen and Larsson 2004) would forage further from the colony and feed at a higher trophic level than females. Males should thus forage predominantly at sea, given that $\delta^{13}C$ and $\delta^{15}N$ are known to be positively correlated (Inger and Bearhop 2008), while females would be expected to focus on terrestrial habitats. Regarding the stress level (H/L ratio), we assumed that females were generally more stressed than males because of the need to produce and lay eggs. Based on the findings of Sommerfeld et al. (2013) and Ratcliffe et al. (2013), we expected the confounding effects of sex, body mass, and stress level to reflect the complex interactions responsible for sex-specific and/or individual foraging behaviours and habitat use in LBBGs.

Materials and Methods

GPS data loggers

A total of 82 LBBGs were caught during the incubation period at five island breeding colonies in the southern North Sea from 2009 to 2013 (Table 131). The capture process and equipment were as described previously (Corman and Garthe 2014). Two types of GPS data loggers were used (Earth & Ocean Technologies, Kiel, Germany; Catnip Technologies, Hong Kong, China). The attached devices weighed 26 g and 30 g, respectively, corresponding to 3.0–4.1% and 3.0–3.5% of the average body masses of equipped and recaptured females (mean ± SD: 736.3 ± 71.2 g; range: 640–918 g; $n_{females}$ = 20) and males (857.2 ± 59.0 g; range: 769–986 g; n_{males} = 28). The recording interval was usually set to 2 min, but eight devices recorded every 5 min and six devices recorded every 3 min. The equipment remained on the birds for about 16 days, after which 65 gulls were successfully recaptured and their devices removed. Sixteen out of 82 equipped birds were not recaptured because of nest predation or because they refused to continue incubating while the trap was active. One bird lost its device and two of the recovered devices malfunctioned. Another individual only conducted one incomplete trip and the data were therefore not included in the analysis. Thus, we had data of 62 individuals with appropriate tracking data for further sampling.

Sampling

All captured gulls were colour-ringed and weighed to the nearest 1 g during their first capture and recapture. At recapture, blood samples (max. 0.5 ml representing ca. 0.8% of the total blood volume of the captured gulls; gauge needle: 0.40 × 0.20 mm) were taken from the cutaneous ulnar vein and used for sexing (Suh et al. 2011), SIA, and white blood cell (WBC) counts. The sex could not be determined in 10 out of the 62 recaptured individuals with appropriate tracking data because of missing or insufficient blood samples. Body masses were not available for four of all sexed birds as a result of malfunctioning balances. Overall, 48 data sets from individuals of known sex and body mass were included for statistical analyses (Table 11).

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Table 11 Sample sizes of lesser black-backed gulls equipped with GPS data loggers during the incubation period at sites in the southern North Sea

Colony	**Location**	**Year**	**No. of captures**	**No. of sexed recaptures**		**No. of blood samples**		**No. of blood smears**	
				males	females	males	females	males	females
Amrum	54°41'N, 8°20'E	2011	7	3	2	3	2	0	0
		2012	11	3	4	2	4	2	4
Borkum	53°43'N, 7°18'E	2012	10	4	2	4	2	4	1
Juist	53°40'N, 7°04'E	2013	15	4	5	4	5	4	4
Norderney	53°43'N, 7°18'E	2013	14	9	2	9	2	9	2
Spiekeroog	53°46'N, 7°42'E	2009	6	2	0	0	0	0	0
		2010	9	3	3	3	3	0	0
		2012	10	3	3	3	3	3	3
∑			**82**	**31**	**21**	**28**	**21**	**22**	**14**

The main dietary composition of the gulls, as used in the stable isotope mixing model below, was identified from current and former pellet collections (*n* = 120 for each colony) in the respective breeding colonies (Kubetzki and Garthe 2003; Schwemmer et al. 2013). All prey items were assigned to the lowest possible taxon and were collected within the foraging range of the gulls whenever possible, but during different years (Table 12). Marine prey items were caught during several ship-based research surveys. Terrestrial prey items were sampled from regurgitates obtained during field work, or caught at areas similar to the terrestrial foraging sites (Table 12). Each prey item was freeze-dried for SIA. All sampled species were tested for differences in δ^{13}C and δ^{15}N values, and differences among sample sites or years, but no significant differences were detected and the data were therefore pooled (linear models, all *p*-values > 0.07; concerned species: *Pleuronectes platessa*, *Callionymus lyra*).

Table 12 Origin of relevant sampled prey items from LBBGs used for stable isotope analysis

Species	Site	Date	Habitat	*n*	Group
Clupea harengus	53.8283 N, 7.1558 E	06-JUL-2014	offshore	5	Caught as free-swimming fish
Sprattus sprattus	53.8283 N, 7.1558 E	04-JUL-2014	offshore	5	
Callionymus lyra	53.7599 N, 7.1387 E	06-JUL-2014	offshore	1	
	54.4307 N, 7.1175 E	10-AUG-2006		2	
	55.3560 N, -0.2353 W	07-AUG-2005		1	
	55.1972 N, 5.4613 E	09-AUG-2005		1	
Limanda limanda	53.8445 N, 7.6743 E	06-JUL-2014	offshore	5	Discarded fish
Solea solea	55.5865 N, 7.0953 E	21-JUL-2007	offshore	4	
Pleuronectes platessa	54.4152 N, 7.1072 E	09-AUG-2006	offshore	2	
	54.4192 N, 7.0535 E	11-AUG-2005		4	
Gadus morhua	54.3498 N, 7.0828 E	11-AUG-2007	offshore	1	
Merlangius merlangus	53.7599 N, 7.1387 E	06-JUL-2014	offshore	5	
Eutrigla gurnardus	56.6158 N, 5.4057 E	19-JUL-2006	offshore	2	
Trachurus trachurus	53.5210 N, 7.3802 E	06-JUL-2014	offshore	5	
Belone belone	54.3820 N, 7.1930 E	10-AUG-2005	offshore	1	
Liocarcinus holsatus	53.5210 N, 7.3802 E	06-JUL-2014	offshore	5	Swimming crabs
Microtus arvalis	54.2039 N, 8.9285 E	JUL-2014	Marshland	1	Mammals
Arvicola terrestris	54.2039 N, 8.9285 E	JUL-2014	Marshland	1	
Talpa europaea	54.2039 N, 8.9285 E	JUL-2014	Marshland	5	
Staphylinidae sp.	54.0724 N, 8.9797 E	20-AUG-2011	Marshland	5	Insects
Carabidae sp.		02-SEP-2011	Marshland	5	
Lumbricus sp.	53.5298 N, 7.2613 E	24-AUG-2014	Grassland	5	Earthworms

Beetles were captured in pitfall traps filled with ethanol. Marine prey items were sampled during ship-based surveys by the Institute of Sea Fisheries of the Johann Heinrich von Thünen Institute (Federal Research Institute for Rural Areas, Forestry and Fisheries) and the Institute for Hydrobiology and Fishery Science of the University of Hamburg

Foraging trips and habitat use

All trips clearly heading out to sea or to the mainland with the first and last position of the trip being at the breeding colony were defined as foraging trips. Trips shorter than 2 km from the nest (beeline) were assumed to be for preening and were therefore excluded. All localizations during nest attendance or resting within or near the breeding colonies were excluded from further analyses. Any incompletely recorded trip was excluded from further analyses (n_{trips} = 10). The parameters used to describe foraging behaviours were trip duration, maximum distance to nest, and total distance flown (R package trip 1.1.18). The habitat type was specified visually by assigning all recorded localizations to either sea or land (mainland/islands) using ArcGIS 10.0 (ESRI 2011), and by calculating the relevant proportions per trip (range: 0–1, marine–terrestrial).

We analysed habitat use by calculating the utilization distribution (UD, 50% and 95%) of each individual via the biased random bridge approach (Benhamou 2011; R package adehabitatHR 0.4.11), in which animals move using biased random walks allowing for time-dependent successive relocations by supposing drift between them. We calculated the areas

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that were exploited for a long time by the same individual (i.e. intensity distribution, ID), and frequently visited areas (recursion distribution, RD). These measurements characterize potentially profitable foraging areas that were exploited intensively by the gulls (Benhamou and Riotte-Lambert 2012). We used the 50% and 95% UD areas (km²) to estimate habitat use, and the 30% ID and RD areas to identify important foraging areas, respectively (Benhamou and Riotte-Lambert 2012).

Stable isotope analyses

SIA has been used to analyse the trophic ecology of seabirds (Inger and Bearhop 2008). In particular, the carbon and nitrogen isotopic ratios can be used to identify the foraging habitat and trophic level, respectively, utilised by individual birds. Low δ^{13}C ratios indicate foraging in terrestrial habitats and high values imply foraging in marine habitats, while high δ^{15}N ratios indicate a high trophic level (Inger and Bearhop 2008; Masello et al. 2010; Ceia et al. 2014b). Isotopic ratios from blood samples (red blood cells, RBC) integrate the bird's diet over the preceding 3 weeks, and thus reflected the gulls' diet throughout the period when the loggers were attached.

Stable isotopes in RBC in the current study were analysed at the Leibniz Institute for Zoo and Wildlife Research, Berlin, Germany (technical details for SIA in e.g., Masello et al. 2010; Masello et al. 2013). In the absence of species-specific trophic enrichment factors, we used averaged values from herring (*L. argentatus*) and great black-backed gulls (*L. marinus*) (−0.06 for $\delta\ ^{13}$C, +2.75 for $\delta\ ^{15}$N) calculated by Steenweg et al. (2011), both of which have similar physiologies, diets, and feeding strategies to LBBGs (Olsen and Larsson 2004).

White blood cell counts

Leukocyte profiles in blood films provide an indirect measure of glucocorticoid hormone levels, increases in which result in characteristic changes in leukocyte profiles. These changes can thus be quantified and linked to glucocorticoid hormone levels (Davis et al. 2008). An increase in heterophils may reflect infection, inflammation, or stress, while lymphocytes are predominantly responsible for regulating immune defence and immunoglobulin production (e.g. Davis et al. 2008; Clark et al. 2009). Chronic stress (e.g., food shortage, long-lasting bad weather conditions) will thus increase the proportion of heterophils, reflected by a relatively high H/L ratio.

We produced peripheral blood films (n_{birds} = 36, no. of inappropriate blood films: 13; Table 11) on microscope slides using the two-slide wedge method (Clark et al. 2009). Whenever possible, we produced two blood films per individual to ensure repeatability of counts (Nakagawa and Schielzeth 2010). Slides were air-dried and stained with Wright-Giemsa stain (Samour 2005) and the numbers of heterophils and lymphocytes were counted under a light microscope (1000× magnification, oil immersion) (Clark et al. 2009). Cells on each slide were counted until 100 leukocytes had been counted (Lobato et al. 2005; Davis et al. 2008; Dehnhard et al. 2011). Each blood film was counted independently by two different people, and twice by one of them to minimize miscounting and maximize repeatability. We calculated the H/L ratio based on these counts (Davis et al. 2008).

Statistical analyses

All statistical analyses were carried out using R 3.1.1 (R Development Core Team 2014). We analysed sex-specific foraging patterns using a linear mixed model (LMM) approach (Faraway 2006) with sex and body mass, or the interaction between sex and body mass, respectively, as explanatory variables. LMMs were performed based on the restricted maximum likelihood criterion (R package lme4 1.1-6). We conducted separate models with a Gaussian error distribution for the following response variables: trip duration, maximum distance to nest, total distance flown, proportion of time spent in terrestrial/marine flights and flights during the day or at night, sizes of 95% and 50% UD, and 30% ID and RD areas, δ^{13}C, δ^{15}N, and H/L ratio. The first three variables were log-transformed, proportion data were arcsine-transformed, and the four UD parameters were square-root-transformed to achieve normality. For a better comparison of the effect sizes, body mass was z-transformed. In all models, colony was treated as random factor to make assumptions at the population level and to account for inter-colony variances in the respective variables not explained by the fixed effects. Individual bird identity was included as a random factor for all variables with repeated measures per bird (i.e., the first five variables listed above), to avoid pseudo-replication. We accounted for between-year variances by including year as an additional random factor where relevant, according to Akaike's information criterion (AIC; Burnham and Anderson 2004).

We used non-informative priors for the coefficients and variance parameters (Korner-Nievergelt et al. 2015). Posterior distributions were obtained by directly simulating 5000 values from the joint posterior distributions of the model parameters (Gelman and Hill 2006; R package arm 1.7-03). The symmetric 95% credible intervals (i.e., 2.5 and 97.5% quantiles) and the means of the simulated values from the joint posterior distributions were used as estimates (Korner-Nievergelt et al. 2015). We inspected residual plots of all models visually to ensure independent and identically-distributed residuals and random effects, and the absence of temporal or spatial autocorrelation.

We estimated the proportion of each food source represented in the LBBG diet using a stable isotope mixing model (R package siar 4.2; for pros and cons see Bond and Diamond 2010; Parnell et al. 2013). We combined all prey taxa into six groups of sources (Table 12) according to the recommendations of Phillips et al. (2014). We then compared isotopic niches (Newsome et al. 2007) between male and female birds using Stable Isotope Bayesian Ellipses in R (SIBER; Jackson et al. 2011). We accordingly estimated the standard ellipse areas corrected for small sample sizes (SEAc) and the Bayesian estimate SEAb (number of posterior draws: 10,000).

The impact of the H/L ratio on either study parameter mentioned above was examined in separate LMMs (predictors: interactions of sex × body mass × H/L ratio; $n_{birds} = 36$; Table

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14). The repeatability (Nakagawa and Schielzeth 2010) of the WBC counts was tested (R package rptR 0.6.405) and all WBC counts were significantly repeatable (LMM, all $P < 0.05$).

Results

Device effects

Data loggers were streamlined and their total attachment mass was 3–5% of the birds' body mass (Wilson and McMahon 2006; Barron et al. 2010; Dixon 2011; but see Vandenabeele et al. 2012) to minimize their impact on flight energetics. Total bird-handling time was ≤10 min. The body mass of the birds decreased during the equipped period (before, mean ± SD: 809.4 ± 88.3; after, 783.4 ± 79.8), though the difference was not significant (Kruskal–Wallis test, $\chi^2 = 1.7$, df = 1, $P = 0.2$, $n = 48$).

Body mass decreased in 31 individuals (range: 0.1–23.3%) and increased in 17 (range: 0.5–12.2%) throughout the study period. Altogether, 15 of the 82 equipped gulls (18.3%) lost their clutches as a result of predation, and two individuals could not be recaptured because they refused to continue incubating while the trap was over their clutch. We confirmed chick hatching in the remaining individuals and detected no abnormal behaviours during the fieldwork period.

There was no significant difference in H/L ratios between equipped ($n = 36$) and unequipped birds ($n = 3$) at the end of the tracking period, suggesting that equipped birds were no more stressed than unequipped ones, though the unequipped sample size was small. A total of 34 equipped birds were subsequently recorded during migration or at their wintering grounds over several years, owing to their colour bands, with further readings of colour bands at some breeding colonies. We thus considered that the GPS devices had a relatively small effect on the gulls, but we could not completely exclude the possibility of behavioural or/and physiological effects.

Foraging trips

Overall, 52 equipped LBBGs ($n_{males} = 31$; $n_{females} = 21$) conducted 616 foraging trips targeting land and/or sea (Fig. 8a, b). Males performed 332 foraging trips with 86 exclusively terrestrial trips (25.9%), 81 exclusively marine trips (24.4%), and 165 mixed trips (49.7%). Females carried out 96 land trips (33.8%), 50 sea trips (17.6%), and 138 (48.6%) trips targeting both habitat types.

Body mass (at capture) differed significantly between the sexes (mean ± SD, males: 857 g ± 59 g, females: 736 g ± 71 g; one-way ANOVA, $F_{1,45} = 40.24$, adj. $R^2 = 0.46$, $n_{birds} = 48$, $P < 0.0001$), though the individual variation (males: 769–986 g; females: 640–918 g) within each sex was higher than the average between-sex difference (121 g).

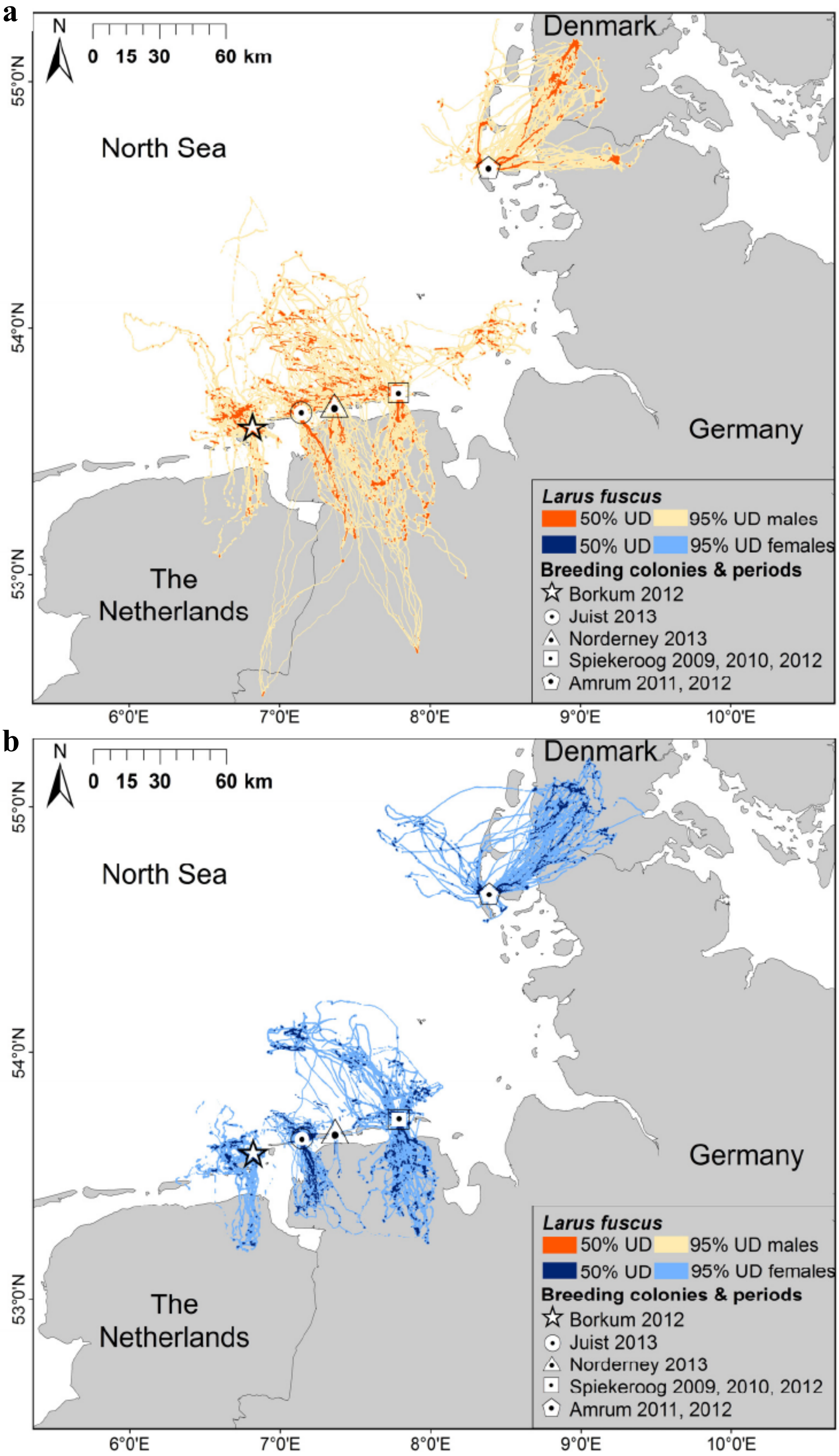

Fig. 8 Foraging-habitat use in male (orange) and female (blue) LBBGs in the southern North Sea. 95% (light colours) and 50% (intense colours) utilization distributions (UDs) in **a** males and **b** females

Males showed longer trip durations, total distances, and maximum distances from the colony, though these differences were not significant (Table 13). None of the parameters were affected by body mass (Table 13). The generally higher proportion of nest attendance by males compared with females was independent of their individual body mass. Female nest attendance decreased significantly with increasing body mass (Table 13). The proportion of terrestrial positions was generally higher for females (Table 13, Fig. 9), indicating that female gulls used terrestrial habitats more frequently than males. Both sexes foraged mainly during daylight (independent of the habitat visited), though females flew slightly more during the day than males (Table 13).

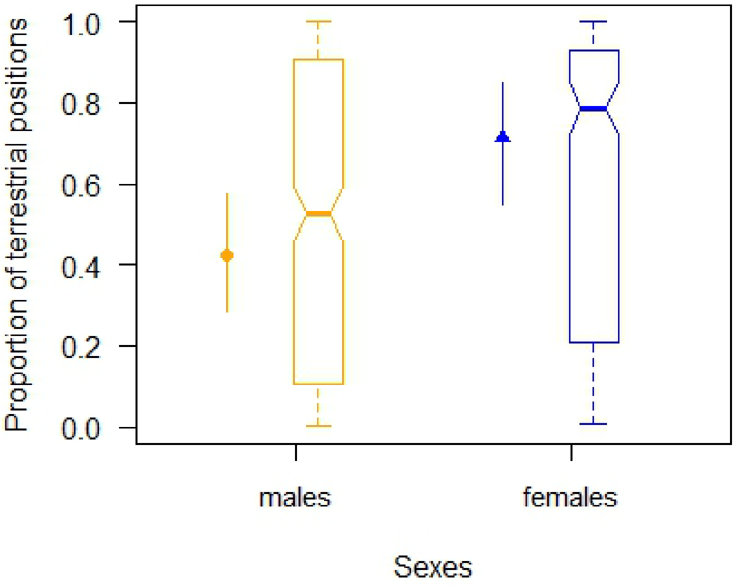

Fig. 9 Proportion of terrestrial positions for male (orange circle) and female (blue triangle) LBBGs. Boxes represent 50% of the data between the first (25%) and third (75%) quartile. The horizontal black line indicates the median. Upper and lower whiskers represent 25% of the remaining data, respectively. Orange circles and blue triangles represent the estimated means derived from Linear Mixed Models including the symmetric 95% credible interval

Habitat use

The 95% and 50% UD areas showed little overlap between males and females (Fig. 8a, b), while the 30% RD and, especially the ID areas (representing the areas of active foraging) were sexually distinct (Fig. 8c). The average overlap of ID areas within each sex was also very low (mean ± SD; within females: 0.010 ± 0.034; within males: 0.001 ± 0.003; UD overlap indices: Fieberg and Kochanny 2005) indicating individual foraging-site specialization. Males generally utilized and foraged in larger areas than females (Table 13). The relationships between these areas and body mass differed within the sexes: areas decreased with increasing body mass in males, but increased with increasing body mass in females (Table 13).

Table 13 Effects of sex, body mass, and the interaction sex × body mass on foraging trip and blood parameters in incubating LBBGs (n = 48). Estimated model coefficients (fixed effects) of linear mixed models are shown

	Males (n = 31)	**Females (n = 21)**	**Prob (m>f)**	**Sex**	**Body mass**	**Sex × body mass**	**Intercept**	**Inter-colony SD**	**Inter-bird SD**	**Inter-year SD**	**Residual SD**
	Est. mean (95% Crl)	**Est. mean (95% Crl)**		**Mean (95% Crl)**	**Mean (95% Crl)**	**Mean (95% Crl)**	**Mean (95% Crl)**	**SD (95% Crl)**	**SD (95% Crl)**	**SD (95% Crl)**	**SD (95% Crl)**
Trip duration [log(h)]	7.37 (5.86–9.19)	6.24 (4.83–8.10)	0.80	-0.16 (-0.55–0.22)	-0.14 (-0.33–0.06)	-	2.00 (1.77–2.22)	0.06 (0.03–0.11)	0.37 (0.31–0.44)	-	0.77 (0.73–0.82)
Max. distance to nest [log(km)]	25.60 (18.48–35.24)	19.43 (13.67–24.49)	0.90	-0.28 (-0.72–0.16)	-0.08 (-0.31–0.14)	-	3.24 (2.92–3.56)	0.26 (0.16–0.28)	0.42 (0.35–0.49)	-	0.67 (0.64–0.71)
Total distance flown [log(km)]	81.83 (61.27–110.29)	60.94 (43.86–85.33)	0.92	-0.30 (-0.71–0.13)	-0.13 (-0.34–0.09)	-	4.41 (4.12–4.70)	0.22 (0.13–0.32)	0.41 (0.34–0.47)	-	0.73 (0.69–0.77)
Prop. of nest attendance [arcsine]	0.59 (0.55–0.63)	0.54 (0.51–0.58)	1	-0.05 (-0.07– -0.02)	0.001 (-0.01–0.02)	**-0.02** **(-0.04– -0.001)**	0.87 (0.84–0.91)	0.04 (0.04–0.05)	-	-	0.08 (0.07–0.08)
Prop. of terrestrial pos. [arcsine]	0.45 (0.30–0.60)	0.67 (0.51–0.82)	0.02	**0.23** **(0.01–0.46)**	0.07 (-0.04–0.18)	-	0.73 (0.58–0.88)	0.10 (0.05–0.16)	0.21 (0.18–0.25)	-	0.40 (0.38–0.43)

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Prop. of daylight pos. [arcsine]	0.81 (0.75–0.87)	0.92 (0.86–0.96)	0.02	**0.15** **(0.01–0.29)**	0.02 (-0.05–0.09)	-	1.13 (1.05–1.20)	Not assessable	0.12 (0.10–0.15)	-	0.36 (0.34–0.38)
95% UD [sqrt(km²)]	377.86 (265.63–503.93)	343.49 (237.06–467.88)	0.91	-0.90 (-2.28–0.50)	-1.16 (-1.98– -0.36)	**2.07** **(0.93–3.27)**	19.38 (16.30–22.45)	2.58 (1.45–3.86)	-	2.15 (1.04–3.24)	4.58 (4.32–4.86)
50% UD [sqrt(km²)]	70.63 (48.44–96.06)	68.81 (46.42–95.26)	0.63	-0.11 (-0.79–0.55)	-0.54 (-0.92– -1.14)	**1.53** **(0.96–2.09)**	8.39 (6.96–9.80)	1.13 (0.65–1.71)	-	1.11 (0.69–1.72)	2.21 (2.09–2.34)
30% ID [sqrt(km²)]	40.01 (28.05–54.42)	37.22 (25.29–51.57)	0.82	-0.23 (-0.71–0.27)	-0.17 (-0.45–0.11)	**0.48** **(0.05–0.90)**	6.33 (5.30–7.38)	1.03 (0.59–1.59)	-	0.62 (0.31–0.99)	1.61 (1.52–1.71)
30% RD [sqrt(km²)]	47.49 (33.22–61.72)	46.15 (31.45–63.53)	0.62	-0.10 (-0.69–0.49)	-0.48 (-0.84– -0.13)	**1.11** **(0.60–1.64)**	6.90 (5.76–8.05)	1.10 (0.58–1.67)	-	0.68 (0.40–1.09)	2.02 (1.91–2.14)
$\delta^{13}C$ (‰)	-19.44 (-22.86– -20.08)	-21.50 (-20.13– -18.08)	1	-2.06 (-2.55– -1.59)	-0.82 (-1.10– -0.53)	**0.58** **(0.16–1.02)**	-19.43 (-20.80– -18.08)	1.40 (1.02–2.17)	-	0.73 (0.36–1.18)	1.67 (1.58–1.77)
$\delta^{15}N$ (‰)	15.08 (13.69–16.44)	13.59 (12.19–14.97)	1	**-1.49** **(-1.98– -0.98)**	-0.002 (-0.24–0.24)	-	15.07 (13.69–16.44)	1.62 (1.07–2.56)	-	0.43 (0.22–0.75)	1.67 (1.58–1.77)
H/L ratio	0.43 (0.36–0.50)	0.50 (0.43–0.57)	0	0.07 (0.03–0.12)	-0.09 (-0.12– -0.06)	**0.36** **(0.31–0.40)**	0.43 (0.35–0.50)	0.08 (0.07–0.10)	-	-	0.13 (0.12–0.14)

CrI = credible interval; est. mean = estimated mean; Prob = posterior probability that the parameter is greater in males than in females; sqrt = square-root transformed; Prop.= proportion; pos. = GPS positions

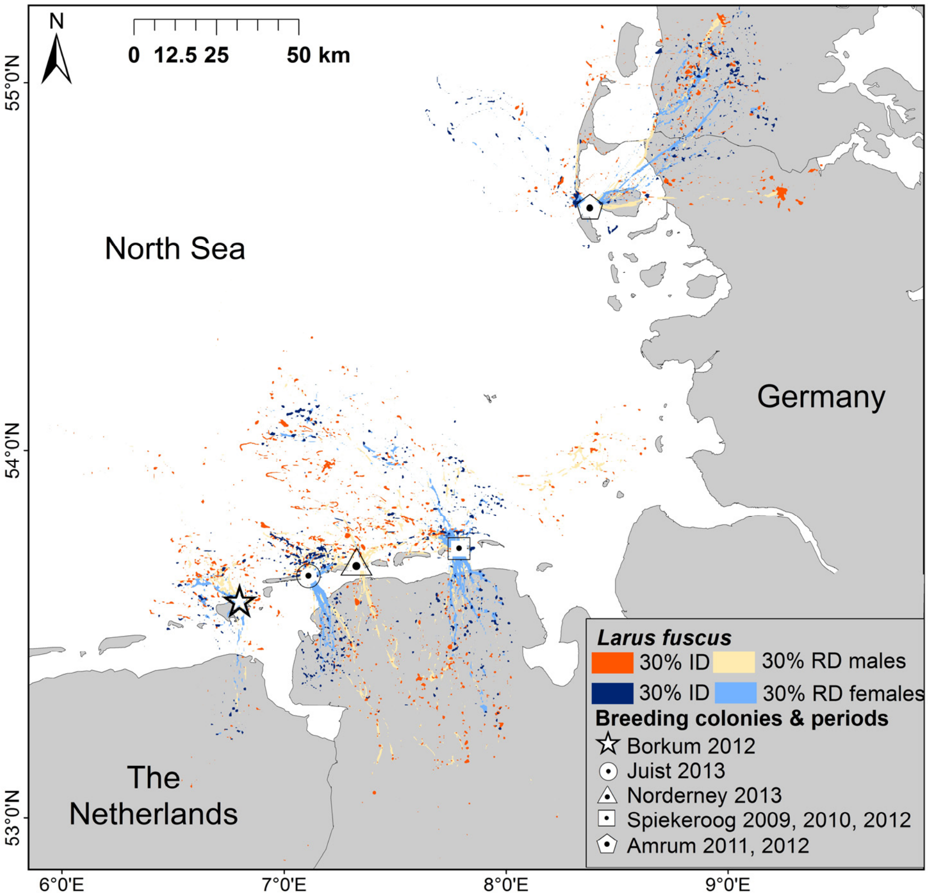

Fig. 10 Foraging-habitat use in male (orange) and female (blue) LBBGs in the southern North Sea. 30% intensity distribution (ID, intense colours) and 30% recursion distribution (RD, light colours) for both sexes

Stable isotope analyses

Females had significantly lower $\delta^{13}C$ signals, indicating more terrestrial feeding than males (Table 13), and simultaneously fed at a lower trophic level than males (Table 13). $\delta^{13}C$ decreased with increasing body mass in both sexes, though the relationship was more apparent in males than in females. Body mass had no influence on $\delta^{15}N$. However, the prey composition derived from SIAR differed only slightly between males and females (Fig. 11). Swimming crabs represented the highest proportion of prey items in the diet of both sexes. However, females had a higher proportion of earthworms and beetles (i.e., terrestrial prey), while males focused slightly more on marine prey. We were unable to detect differences in frequencies of free-swimming and discarded fish in the diet of either sex from the mixing model (Fig. 11).

SIBER analyses of the carbon and nitrogen values supported the above results, with females demonstrating less variation in isotopic niche width than males, which showed a significantly larger and slightly more marine isotopic niche ($SEAb_{males}$ = 6.95, $SEAb_{females}$ = 2.97; posterior probability $SEAb_{males} > SEAb_{females}$: 0.98) (Fig. 12). Males generally consumed a broader spectrum of prey along both gradients of isotopic signatures than females. Both foraging niches overlapped to some degree (area of overlap: 2.38). A more marine diet was

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generally associated with a higher trophic level (Fig. 12).

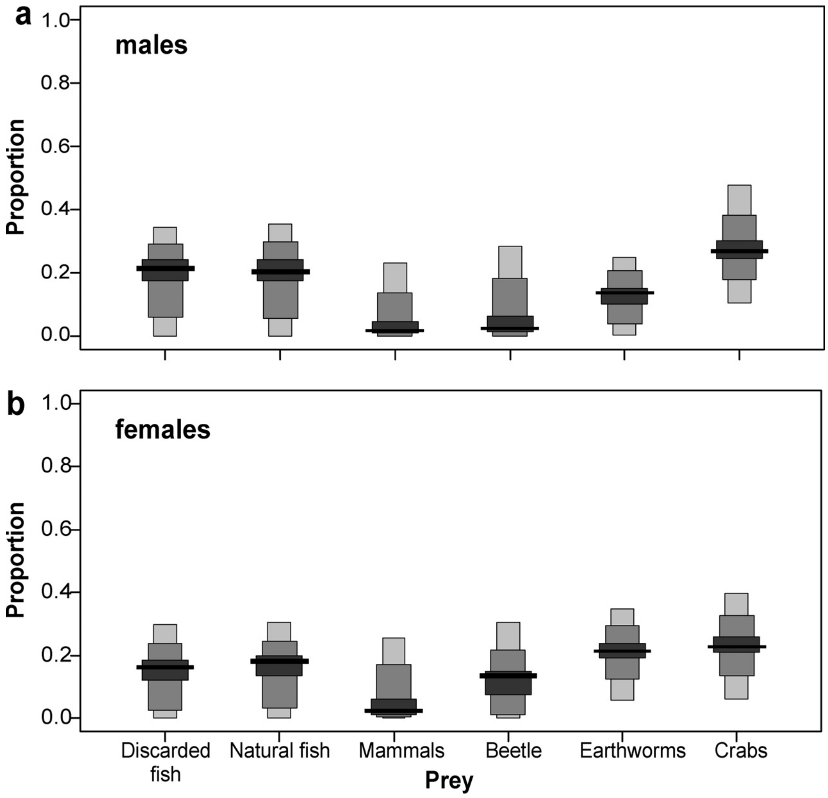

Fig. 11 Proportions of the main food sources, based on $\delta^{13}C$ and $\delta^{15}N$ in red blood cells from **a** male and **b** female LBBGs breeding on the southern North Sea coast during incubation. Decreasing grey scale and bar width represent 5%, 25%, 75% and 95% probability intervals derived from stable isotope mixing model, Stable Isotope Analysis in R (R package siar 4.2)

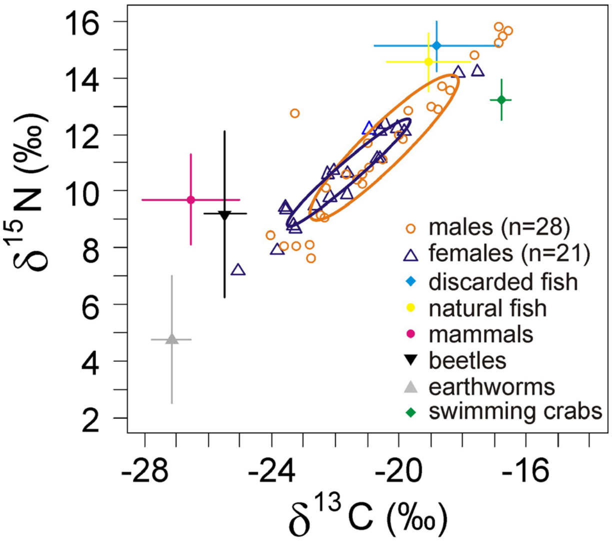

Fig. 12 Isotopic niche width based on stable isotope signatures ($\delta^{13}C$ and $\delta^{15}N$) in red blood cells, and isotopic signatures (mean ± SD) of the six main food sources in male (orange circles) and female (blue triangles) LBBGs from different breeding colonies on the southern North Sea coast during incubation periods from 2009 to 2013. Ellipses indicate the area of the standard ellipses (SEAc, 40% CrI) following Jackson et al. (2011)

Individual body mass and H/L ratio

Leukocytes comprised 23.3% heterophils (mean ± SD, 23.5% ± 12.4%) and 72.6% lymphocytes (72.5% ± 13.3%), with other granulocytes accounting for the remainder. The interaction of sex × body mass had a marked influence on the H/L ratio: on average, females had higher H/L ratios (i.e., were generally more stressed) than males (Table 13). However, the H/L ratio decreased with increasing body mass in males, but increased in females (Fig. 13). H/L ratio included as an additional model predictor affected most of the considered parameters, and changed the effects of sex and mass or their interaction on these parameters (Tables 13, 14).

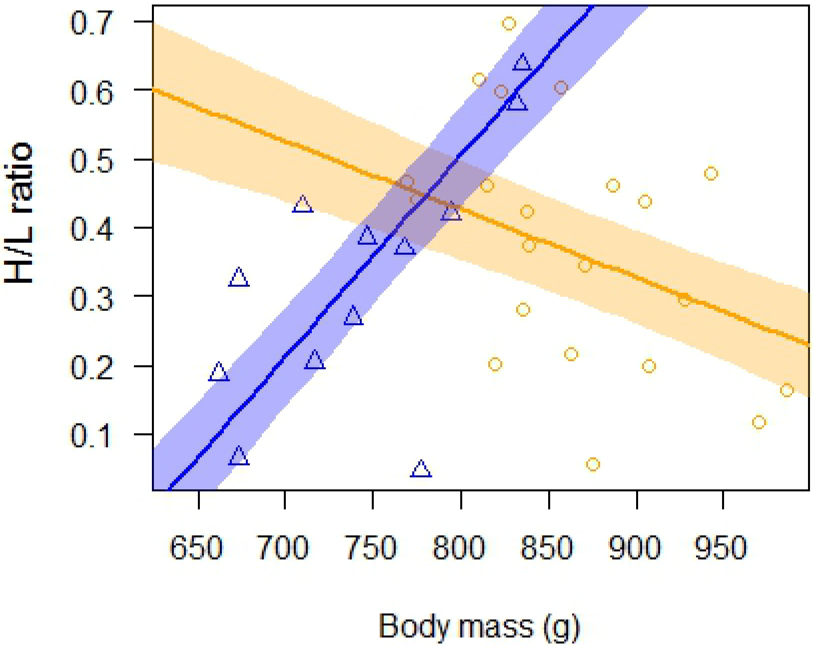

Fig. 13 Interrelated effect of sex × body mass on H/L ratio in incubating lesser black-backed gulls (orange: males; blue: females). Solid lines represent the estimated effects with the corresponding 95% credible intervals

Males and heavy individuals made longer-lasting and further trips than lighter individuals and females, accounting for stress in the model. Females with higher H/L ratios (higher stress) made longer-lasting and further trips from the colony (Table 13) and utilized larger areas than females with lower H/L ratios (Fig. 14). The converse was true in males: trip duration, maximum distance to the colony, and the four utilization areas decreased with increasing H/L ratios (Table 13; Fig. 14). Stressed birds flew shorter total distances with increasing body mass, but this effect disappeared at low stress levels (Tables 14, Fig. 15).

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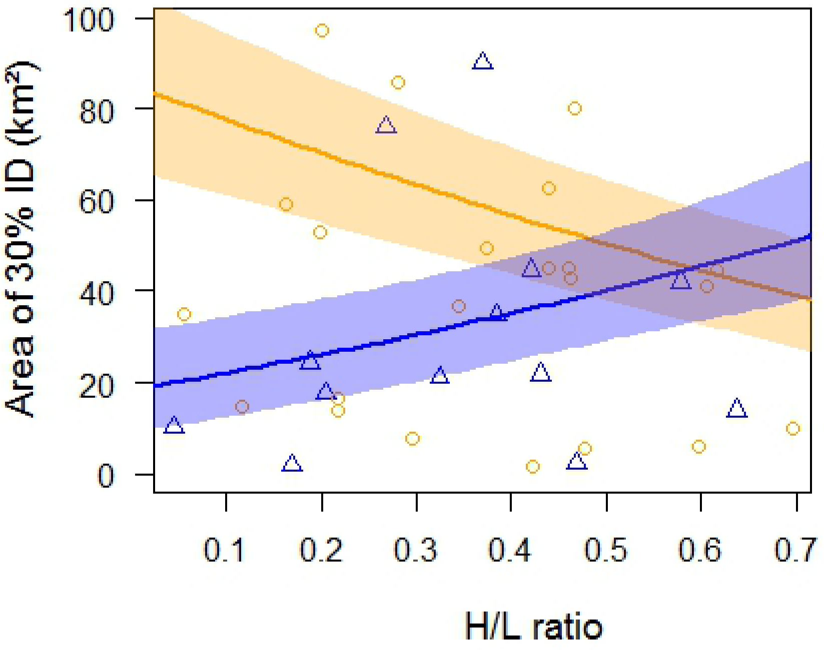

Fig. 14 Interrelated effects of sex × H/L ratio on the 30% intensive distribution (ID) area of incubating LBBGs (orange: males; blue: females). Solid lines represent the estimated effects with the corresponding 95% credible intervals

The proportion of nest attendance increased in stressed males but decreased in stressed females with increasing body mass (Table 14, Fig. 16), while body mass had only a slight effect on nest attendance in unstressed birds of both sexes.

Table 14 Estimates of the effects of sex, body mass and the interactions sex × body mass, sex × H/L ratio, sex × body mass × H/L ratio on foraging trip and blood parameters in incubating LBBGs (*n* = 36). Estimated model coefficients (fixed effects) of linear mixed models are shown

	Sex	**Body mass**	**H/L ratio**	**Sex × body mass**	**Sex × H/L ratio**	**Body mass × H/L ratio**	**Sex × body mass × H/L ratio**	**Intercept**	**Inter-colony SD**	**Inter-bird SD**	**Inter-year SD**	**Residual SD**
	Mean (95% Crl)	**Mean (95% Crl)**	**Mean (95% Crl)**	**Mean (95% Crl)**	**Mean (95% Crl)**	**Mean (95% Crl)**	**Mean (95% Crl)**	**Mean (95% Crl)**	**SD (95% Crl)**	**SD (95% Crl)**	**SD (95% Crl)**	**SD (95% Crl)**
Trip duration [log(h)]	-1.05 (-2.02– -0.12)	**-0.37** **(-0.64– -0.12)**	-0.96 (-2.09–0.15)	-	**2.14** **(0.22–4.13)**	-	-	2.51 (1.96–3.07)	Not assessable	0.33 (0.26–0.40)	-	0.78 (0.73–0.84)
Max. distance to nest [log(km)]	-0.28 (-0.74–0.19)	0.14 (-0.26–0.53)	0.34 (-0.60–1.32)	-	-	-	♂: **-1.34** **(-2.66– -0.05)** ♀: -1.03 (-2.72–0.69)	3.24 (2.72–3.74)	0.26 (0.14–0.39)	0.38 (0.30–0.46)	-	0.70 (0.65–0.75)
Total distance flown [log(km)]	-0.33 (-0.75–0.11)	0.10 (-0.24–0.45)	0.15 (-0.73–1.02)	-	-	-	♂: **-1.41** **(-2.62– -0.20)** ♀: -0.94 (-2.53–0.54)	4.51 (4.05–4.97)	0.22 (0.10–0.36)	0.33 (0.26–0.40)	-	0.74 (0.69–0.79)
Prop. of nest attendance [arcsine]	-0.08 (-0.13– -0 02)	-0.06 (-0.09– -0.03)	-0.02 (-0.11–0.07)	0.01 (-0.04–0.05)	0.11 (-0.01–0.23)	0.34 (0.24–0.43)	**-0.40** **(-0.53– -0.27)**	0.84 (0.78–0.90)	0.06 (0.05–0.07)	-	-	0.06 (0.06–0.07)
Prop. of terrestrial pos. [arcsine]	**0.30** **(0.04–0.54)**	0.04 (-0.09–0.17)	-0.19 (-0.66–0.28)	-	-	-	-	0.77 (0.54–1.00)	0.05 (0.02–0.08)	0.21 (0.17–0.26)	-	0.41 (0.39–0.44)
Prop. of daylight pos. [arcsine]	**0.19** **(0.02–0.36)**	0.05 (-0.04–0.14)	0.18 (-0.15–0.51)	-	-	-	-	1.01 (0.85–1.17)	3.3E-09 (1.2E-09–6.3E-09)	0.13 (0.10–0.16)	-	0.37 (0.35–0.40)

95% UD [sqrt(km²)]	-11.27 (-14.16– -8.36)	-3.67 (-4.55– -2.77)	-11.00 (-14.29– -7.73)	**4.33** **(2.67–6.02)**	**17.13** **(11.34–22.66)**	-	-	27.07 (24.42–29.80)	2.94 (2.31–3.99)	-	4.0E-07 (1 3E-08–1.3E-06)	3.80 (3.55–4.06)
50% UD [sqrt(km²)]	-4.89 (-6.50– -3 25)	-1.05 (-1.76– -1.14)	-3.19 (-5.26– -1.03)	**1.76** **(0.94–2.60)**	**7.29** **(3.97–10.49)**	**-2.35** **(-4.30– -0.38)**	-	11.40 (10.09–12.72)	1.13 (0.65–1.71)		2.0E-07 (1 0E-08–6.4E-07)	1.83 (1.72–1.96)
30% ID [sqrt(km²)]	-4.94 (-6.02– -3 89)	-1.21 (-1.53– -0.88)	-4.30 (-5.46– -3.11)	**1.19** **(0.57–1.81)**	**8.38** **(6.34–10.39)**	-	-	9.26 (8.19–10.31)	1.20 (0.94–1.63)	-	Not assessable	1.37 (1.28–1.47)
30% RD [sqrt(km²)]	-3.16 (-4.52– -1.78)	-0.71 (-1.34– -0.10)	-2.86 (-4.74– -0.96)	**2.62** **(1.90–3.31)**	**3.66** **(0.87–6.36)**	**-3.34** **(-5.11– -1.55)**	-	9.70 (8.39–10.96)	1.30 (1.04–1.75)	-	Not assessable	1.53 (1.43–1.64)
δ^{13}C (‰)	-5.47 (-6.84– -4.18)	-0.20 (-1.00– -0.58)	-1.85 (-0.30–4.06)	-2.63 (-3.82– -1.48)	5.28 (2.46–8.14)	4.64 (-7.18– -2.09)	**7.36** **(3.98–10.73)**	-20.12 (-21.64– -18.67)	1.66 (1.38–2.23)	-	Not assessable	1.51 (1.41–1.62)
δ^{15}N (‰)	-4.03 (-5.29– -2.79)	2.35 (1.64–3.06)	5.89 (3 86–7.85)	-5.24 (-6.34– -4 21)	2.65 (-0.004–5.20)	-9.69 (-12.10– -7.35)	**12.12** **(8.97–15.40)**	12.81 (11.41–14.24)	1.55 (1.30–2.10)	-	Not assessable	1.40 (1.31–1.50)

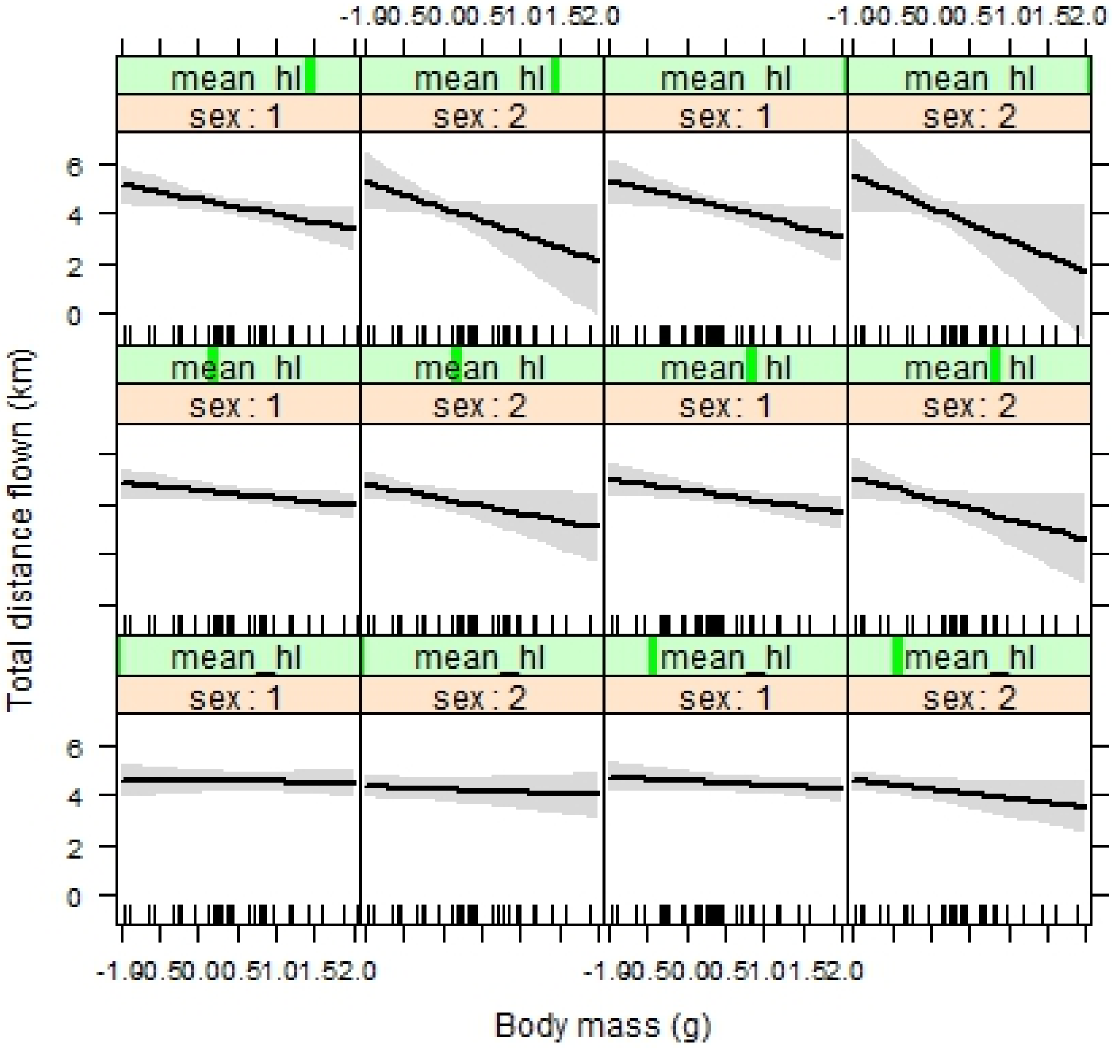

Fig. 15 Interrelated effect of sex × body mass × H/L ratio on the log-transformed total distance flown in incubating lesser black-backed gulls. Body mass was z-transformed. The green marker represents different levels (quartiles) of H/L ratios (right: high; left: low). The solid black lines represent the estimated effects with the corresponding 95% confidence intervals (grey)

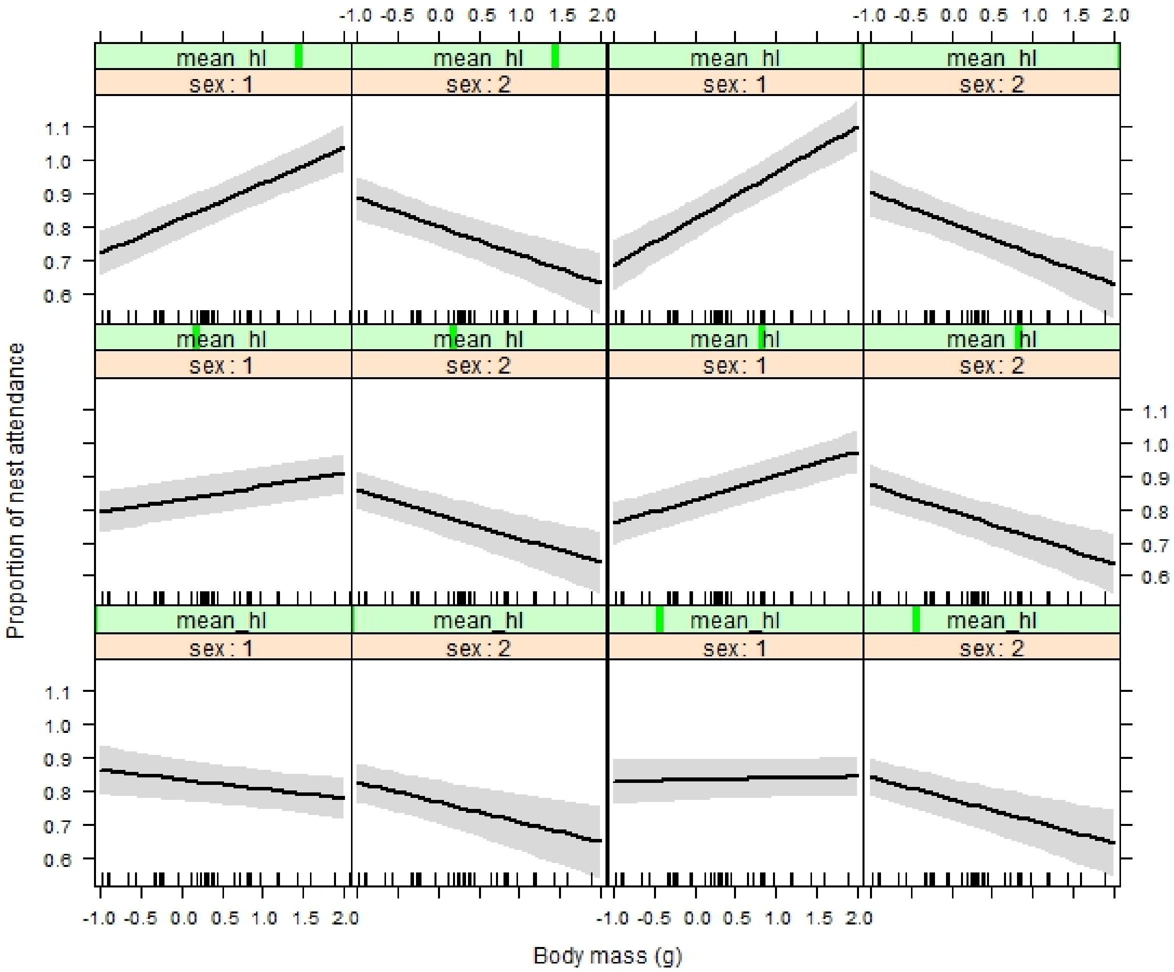

Fig. 16 Interrelated effect of sex × body mass × H/L ratio on arcsine-transformed relative nest attendance in incubating lesser black-backed gulls. Body mass was z-transformed. The green marker represents different levels (quartiles) of H/L ratios (right: high; left: low). The solid black lines represent the estimated effects with the corresponding 95% confidence intervals (grey)

The effect of H/L ratio on the isotopic ratio was related to sex and body mass: $\delta^{13}C$ decreased with increasing body mass in both sexes, independent of the H/L ratio (Table 14, Fig. 17), indicating that heavier birds fed more terrestrially. Trophic level was also affected by the H/L ratio: $\delta^{15}N$ decreased with increasing body mass in stressed individuals of both sexes, indicating that stressed birds fed more on lower trophic-level prey with increasing body mass. This pattern was similar in unstressed females, while trophic level increased with increasing body mass in unstressed males (Table 14, Fig. 18).

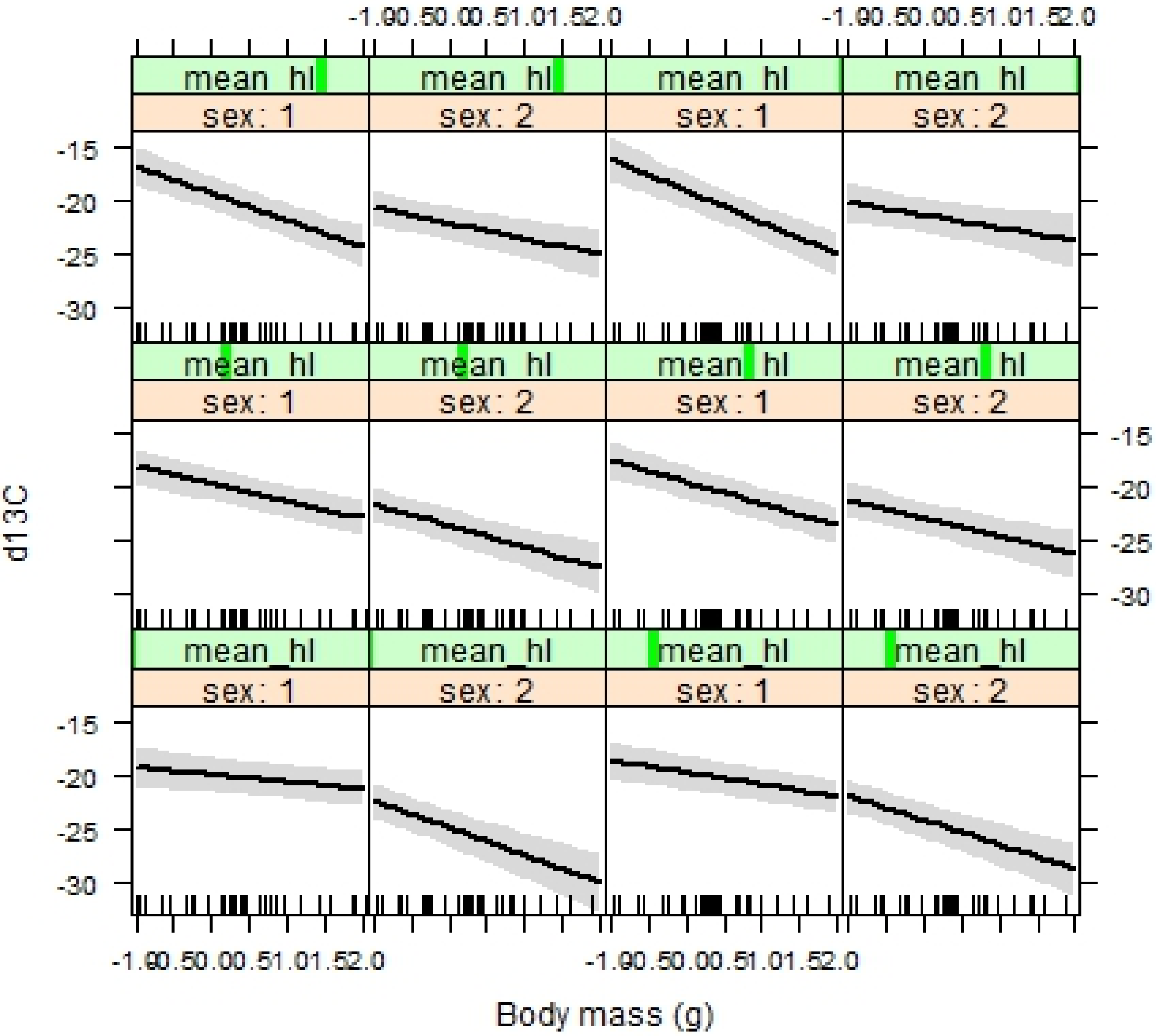

Fig. 17 Interrelated effect of sex × body mass × H/L ratio on δ^{13}C in incubating lesser black-backed gulls. Body mass was z-transformed. The green marker represents different levels (quartiles) of H/L ratios (right: high; left: low). The solid black lines represent the estimated effects with the corresponding 95% confidence intervals (grey)

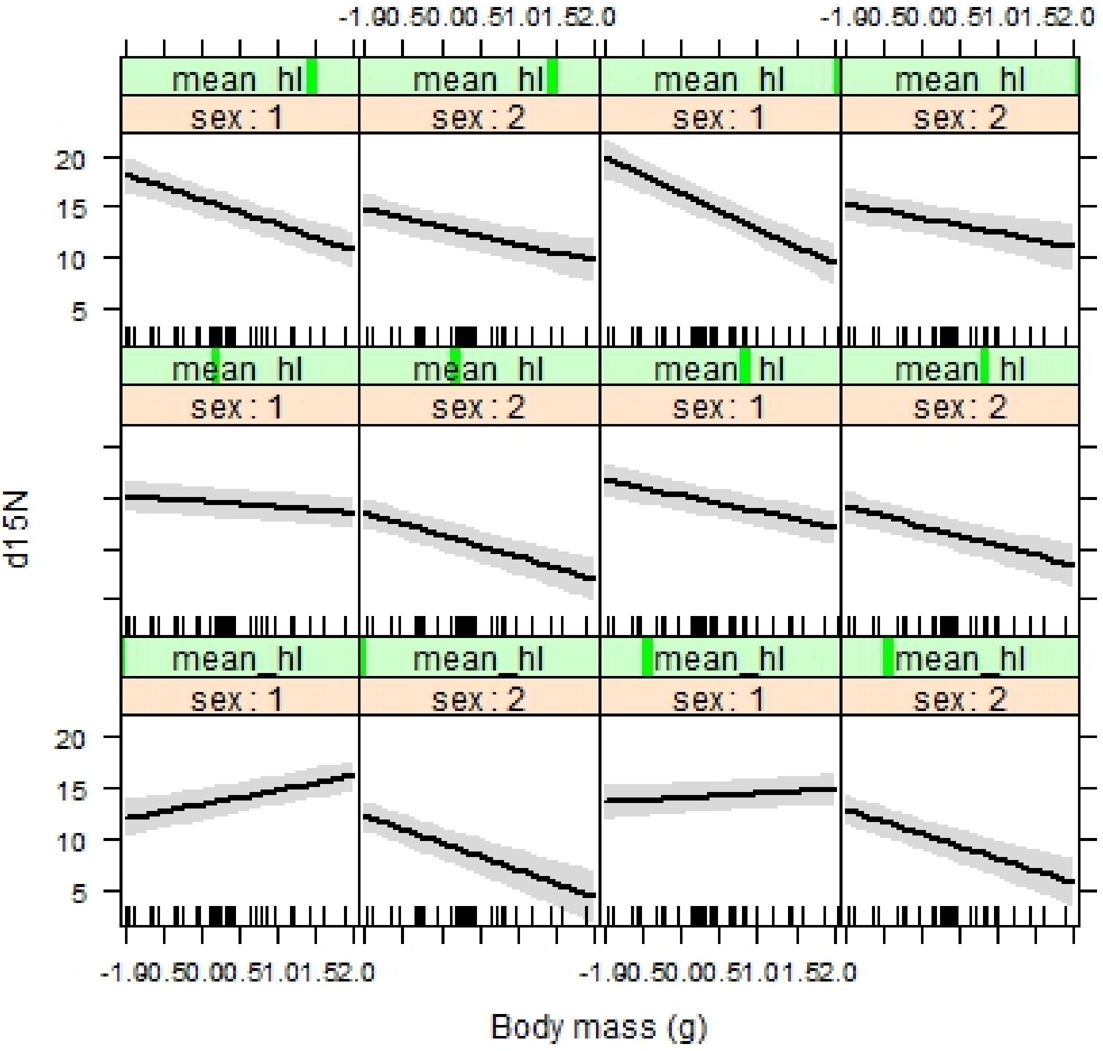

Fig. 18 Interrelated effect of sex × body mass × H/L ratio on $\delta^{15}N$ in incubating lesser black-backed gulls. Body mass was z-transformed. The green marker represents different levels (quartiles) of H/L ratios (right: high; left: low). The solid black lines represent the estimated effects with the corresponding 95% confidence intervals (grey)

Discussion

We investigated sex-specific foraging behaviours in incubating LBBGs using a combination of GPS telemetry, SIA, and WBC counts. Our results revealed spatial segregation of foraging sites in terms of area utilization, and foraging habitat. We identified complex interactions among sex, body mass, and H/L ratio, with largely opposing relationships in males and females. These findings suggest differences in foraging strategies and different means of coping with stress both within and between sexes, depending on individual body mass.

Body mass as measure of body size

The use of body mass as an index of overall body size is controversial (Freeman and Jackson

1990; Piersma and Davidson 1991), but was the only related measure recorded throughout all the study periods and breeding colonies. Size measurements such as wing length were only available for a subset of individuals (*n* = 22), but were not correlated with body mass. This lack of a relationship may be attributable to the small sample size, or may indicate that wing length alone is a poor indicator of body size (Freeman and Jackson 1990; Bosman et al. 2012). We therefore cannot be certain that birds with a high body mass were equivalent to larger birds or birds in good body condition.

Sex-specific habitat segregation

Size-dimorphic seabird species are expected to exhibit spatial segregation between the sexes in association with the greater competitive strength of the larger sex, thus avoiding intraspecific competition (Catry et al. 2006; Quintana et al. 2011; Ludynia et al. 2013). We accordingly found spatially segregated and slightly overlapping foraging areas for male and female LBBGs in most instances. Although there were no significant differences in trip duration or distance from the colony between the sexes, they visited different foraging sites, as shown in various other studies (González-Solís et al. 2000; Ratcliffe et al. 2013; Cleasby et al. 2015). Interestingly, this sex-specific spatial segregation covered two different habitat types, in line with the findings of Camphuysen et al. (2015) who reported that males spent about 80% of their foraging time at sea, whereas females used all available habitat types with similar frequencies. Likewise, a recent study on northern gannets (*Morus bassanus*) found sex-specific habitat segregation across varying tidal mixing regimes, most likely driven by the birds' habitat choice (Cleasby et al. 2015).

The current study found that the most striking differences between marine and terrestrial habitats involved prey distribution and availability: these were patchy and less predictable at sea (Weimerskirch 2007; Ulleweit et al. 2010), but more equally distributed and predictable on land (Palm et al. 2013). However, prey characteristics differ between the sea and land, necessitating different capture methods (surface feeding versus foraging on foot). Furthermore, scavenging within a large (mixed-species) feeding flock is highly competitive, implying a level of stress associated with this type of feeding (Camphuysen 1995; Sotillo et al. 2014). Terrestrial foraging, other than e.g. at landfill sites, may be less arduous because the prey is more evenly distributed (Palm et al. 2013), and competitors are therefore scarcer or spread across a larger area. Capturing terrestrial prey such as earthworms or insects may also be less stressful (Cramp and Simmons 1983). Different, foraging techniques may thus have different energy costs. Furthermore, the contrasting habitat structures at sea and on land (sea surface versus grassland/crops with varying growth heights) may also necessitate different foraging strategies and appropriate physical adaptations (e.g., larger, stronger bill). Thus habitat structure might also affect the energetic costs of foraging.

For all the above reasons, male gulls would be expected to dominate females within scavenging feeding flocks, and be more successful at capturing discards and defending them against competitors (Phillips et al. 2004; Lewis et al. 2005; Catry et al. 2006). However, the 30% ID areas (indicating active foraging; Benhamou and Riotte-Lambert 2012) utilised by the tracked birds revealed that females did fly in the area parallel to the coast utilised by fishing vessels, and at least some individuals seemed to forage there. However, additional data are needed to determine if female gulls scavenged successfully in these areas, or if they were outcompeted by males or other larger species. Moreover, according to the SIA results, the diet of females included a proportion of discarded fish. Likewise, two similar studies on LBBGs from Texel (Netherlands) found that males and females regularly scavenged in mixed feeding flocks (Camphuysen et al. 2015; Tyson et al. 2015), though females seemed to be restricted to the Wadden Sea, while males tended to scavenge offshore. The slight sexual size dimorphism and consequent exclusion of smaller females by larger males (Phillips et al. 2004; Lewis et al. 2005) therefore cannot be the only factor responsible for habitat segregation in LBBGs, as indicated by several previous studies (Lewis et al. 2002; Ludynia et al. 2013; Cleasby et al. 2015).

Nevertheless, some females and males from different breeding colonies regularly foraged at sea and on land, respectively. Interestingly, many of the male terrestrial foraging trips targeted landfills or a meat factory about 135 km from the breeding colonies where several thousand LBBGs, as well as herring gulls, were frequently observed during the incubation period (V. Blüml, pers. comm.). This supports the hypothesis that males might cope better at highly competitive foraging sites than females.

In summary, the results suggest that slightly smaller and lighter female LBBGs tend to forage terrestrially, where prey is easily available and conspecific competition is low, while males concentrate their foraging efforts rather at sea. However, this sex-specific segregation is not absolute.

Dietary segregation

In accordance with previous studies (Cherel et al. 2008; Phillips et al. 2011; Mancini et al. 2013) and our tracking data, SIA supported the existence of sex-specific habitat segregation in LBBGs: males generally had a more marine isotopic signature, indicating feeding at a higher trophic level than females. However, the isotopic niche model showed an overlap between female and male niches, indicating a degree of trophic segregation between the sexes similar to the observed habitat segregation. However, the prey composition indicated that although both sexes frequently ate swimming crabs, females ate higher proportions of earthworms and beetles than males. In this context, it must be kept in mind that certain food items (e.g., terrestrial offal), which were particularly used by some male individuals, were not available and thus could not be included in the model.

Regarding overall prey choice, the present results are in line with classical diet-sampling studies performed in the same area (Kubetzki and Garthe 2003; Schwemmer and Garthe 2005). In addition to avoiding intraspecific competition, differences in prey composition might also imply differences in quality in relation to energy density and nutrient content. However, at least some of the fish species in the diet had a similar nutrient content to earthworms (Hislop et al. 1991; Finke 2002).

Females may have higher energy demands than males associated with the need to produce eggs, and may thus be more stressed than males (Williams 2005; Dehnhard and Hennicke 2013; but see Wojczulanis-Jakubas et al. 2014). This increased demand might apply mainly to certain macro- and micronutrients such as specific amino acids or calcium (Williams 2005). Egg-laying females are also subject to long-term effects such as compromised flight performance due to protein depletion of flight muscles (Monaghan and Nager 1997; Williams 2005). The consequences of egg production might thus also occur later in the breeding period. However, data on the costs of egg production, especially in the long-term, are currently scarce (Williams 2005).

Within-sex differences

In accordance with Lewis et al. (2005), lighter individuals of the same sex tended to make further and longer-lasting foraging trips, possibly because of the lower flight costs associated with reduced body weight. Sex-specific differences in trip length and duration were not influenced by individual body mass, but were affected by individual stress levels. Trip durations in females increased with increasing stress levels, but decreased with increasing stress levels in males, for all UD areas, suggesting that the two sexes reacted differently to persistent, physiological stress. Accordingly, UD areas decreased in males but remained relatively constant in females with increasing body mass. The opposite effects of H/L ratios in males and females may be related to the different parental roles they occupy (Thaxter et al. 2009; Elliott et al. 2010): males are largely responsible for territorial defence (see Burger 1980; Butler and Trivelpiece 1981; Butler and Janes-Butler 1982 for herring and great black-backed gulls) and thus attend their nest more frequently than females, as demonstrated here. Shorter trip duration and length and smaller foraging area in response to stress enable males to return to the nest faster. Males may also concentrate on foraging for relatively predictable discarded fish (Cama et al. 2012; Ulleweit et al. 2010) at shrimping boats close to the colony, to maximize foraging efficiency. Assuming that a high body mass reflects a certain physical strength, heavy males might be more effective than light ones at defending their clutch against neighbours or intruders trying to predate their eggs.

Making shorter foraging trips also reduces flight costs, as long as foraging is efficient (Pennycuick 2008). Stressed males fed more terrestrially with increasing body mass, but this effect vanished as stress levels decreased. Interestingly, the trophic level of the prey also increased with increasing body mass. These results further support the hypothesis that heavy males tend to focus on easily available, anthropogenic waste from terrestrial sites or fisheries, even though free-swimming fish are of higher quality than discarded ones (Grémillet et al. 2008b; but see Morrison et al. 2014). Heavy males thus reduce trip lengths and foraging areas in times of stress to minimise the risk of further stress associated with higher flight costs. However, stressed lighter males that cannot compete effectively within scavenging feeding flocks, but which have lower flight costs, might utilise less-competitive marine sites further from the coast. In contrast, females, which were generally more stressed than males, increased their trip durations and foraging areas with increasing stress levels, thus accruing higher flight costs.

We previously showed that LBBGs performed longer-lasting and further foraging trips when the trips were targeted inland compared with at sea (Corman et al., unpublished data). Higher flight costs over land may be offset by advantageous thermals (e.g. Bryan et al. 1995), which may be especially important for females, which predominantly foraged terrestrially. Females fed more terrestrially and on lower-trophic-level prey with increasing body mass, irrespective of the stress level, suggesting that females have different energetic demands than males (Lewis et al. 2002; Ludynia et al. 2013) that could be largely satisfied by terrestrial prey. However, the differences between terrestrial and marine prey items in terms of specific macro- and/or micronutrients, and the nutrient requirements of both sexes need further clarification. Sex-specific division of labour, as demonstrated in two *Sula* species (Velando and Alonso-Alvarez 2003; Weimerskirch et al. 2009; Sommerfeld et al. 2013), might also occur in LBBGs that demonstrate differences in their parental efforts. However, these previous studies were conducted during chick rearing rather than incubation, and this pattern might thus become more apparent during this later phase of breeding.

In summary, sex-specific foraging behaviour of incubating LBBGs mainly manifests by foraging in segregated habitats. It is likely that this segregation has developed in response to the need to avoid intraspecific competition both within and between the sexes, as well as to individual foraging specialisations, different energetic demands associated with different parental roles, and individual differences in body mass and stress level. These patterns may become even more pronounced during chick rearing, when the adults need to remain closer to the colony, and when stress levels rise as a result of the need to balance chick- and self-provisioning (Weimerskirch et al. 2009; Dehnhard and Hennicke 2013). Further studies are needed to clarify the complex relationships among individual body measurements and stress levels, and their effects on individual and sex-specific foraging behaviours in seabirds.

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Ethics statement

All applicable national and institutional guidelines for the handling and equipping of animals were followed. Birds were caught, ringed and equipped under licenses issued by the National Park Administration of the Wadden Sea National Park of Lower Saxony, the Lower Saxony State Office for Consumer Protection and Food Safety (file number: 33.14-42502-04-11/0666), the State Agency for Agriculture, Environment and Rural Areas Schleswig-Holstein and the Ministry of Energy Transition, Agriculture, Environment and Rural Areas Schleswig-Holstein, Germany (file numbers: V 312-72241.121-37 (34-4/11), V 312-7224.121-37 (80-6/13)).

CHAPTER III:

What flight heights tell us about foraging and potential conflicts with wind farms: a case study in lesser black-backed gulls (*Larus fuscus*)

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What flight heights tell us about foraging and potential conflicts with wind farms: a case study in lesser black-backed gulls (*Larus fuscus*)

Anna-Marie Corman and Stefan Garthe

Abstract

Avian flight heights are currently a focus of interest in terms of assessing possible impacts of offshore and inland wind farms on birds. We therefore analyzed the flight-height distribution in a tracking study of foraging lesser black-backed gulls (*Larus fuscus*) on the southern North Sea coast during the incubation period. We distinguished between marine and terrestrial, nocturnal and diurnal, straight and tortuous, and outbound and inbound flights. Individuals were equipped with specifically-programmed GPS data loggers to ensure accurate flight-height measurements. A total of 89% of recorded fixes were below 20 m above sea level, indicating an overlap between foraging flights and the rotor area of most operating wind turbines. The gulls flew lower over the sea than over land, and lower at night than during the day. Straight commuting flights were higher than tortuous flights, when the gulls were supposed to be foraging. Outbound and inbound flights occurred at similar heights, and flight height was unaffected by wind. This study provides insights into the individual flight-height distribution in a common seabird species throughout a range of foraging behaviors. These results might prove important for developing a comprehensive understanding of bird movements within and around wind farms, and the potential impacts of such wind farms on foraging patterns.

Keywords: flight height, foraging behavior, GPS tracking, *Larus fuscus*, wind energy

Introduction

The relevance of flight heights has recently become a focus of applied research in the context of human pressures, such as collision risks with human constructions (Bevanger 1994; Shamoun-Baranes et al. 2006). In particular, flight height is a key factor for assessing collision risks between flying birds and wind turbines (Garthe and Hüppop 2004; Desholm and Kahlert 2005; Johnston et al. 2013; Furness et al. 2013). A detailed and accurate knowledge of flight heights is therefore essential to allow the impacts of these structures to be assessed. Flight heights depend on several factors (Kahlert et al. 2012), especially weather conditions including wind and rain (Liechti 2006), and time of day (Cooper and Ritchie 1995). For instance, birds fly higher with tailwinds than with headwinds, to utilize wind assistance (Kahlert et al. 2012). However, most existing studies have concentrated on flight heights during migration (Schmaljohann et al. 2008; Klaassen et al. 2011), and data on individual flight heights during the breeding season, especially during foraging, are sparse (Krüger and Garthe 2001; Shamoun-Baranes et al. 2006).

Avian flight heights can be estimated by e.g. optical rangefinders during ship-based surveys (Camphuysen et al. 2004) or land-based sea watching (Krüger and Garthe 2001; Cook et al. 2012), and also using radar (Desholm and Kahlert 2005), digital aerial surveys (Buckland et al. 2012), and tagging with GPS data loggers (Bouten et al. 2013). This last option may be the best suited for tracking individuals during foraging flights over long distances. Compared with the other methods, height measurements made using GPS data loggers are not dependent on daylight or weather conditions, and are not overestimated or underestimated as a result of factors such as the reflective sea surface or visual constraints. However, one disadvantage of GPS data loggers is their relatively low accuracy, which is currently 15 m at best (Ens et al. 2008). In order to improve the accuracy of this technique, the recording interval needs to be as short as possible, with the highest possible satellite coverage. Unfortunately, a short recording interval means loss of battery life, though accuracy and battery life can be maximized by using specifically-programmed GPS data loggers.

Lesser black-backed gulls are opportunistic feeders that forage in offshore and coastal areas, as well as inland (Kubetzki and Garthe 2003), during the day and at night (Camphuysen 1995; Garthe and Hüppop 1996). Hence, there is a potential overlap between the gulls' foraging areas and wind farms, in fact during the whole day. The general and extremely flexible flight style of lesser black-backed gulls (Shamoun-Baranes and van Loon 2006; Klaassen et al. 2011) supports opportunistic foraging behaviors and allows them to adapt to changing weather conditions and to obstacles. That is why they have long been considered less sensitive to collisions with wind turbines compared to other species (Garthe and Hüppop 2004). Recent studies (Shamoun-Baranes and van Loon 2006; Cook et al. 2012; Mendel et al. 2014) have now shown that lesser black-backed gulls indeed fly at “critical” heights overlapping with the rotors swept area of the wind turbines and are therefore well suited to study vertical movements within and around wind farms. Furthermore, since lesser black-backed gulls are common breeding birds of the German North Sea Coast, access to their breeding colonies, as well as their capture, are comparatively easy during the incubation period.

We equipped incubating lesser black-backed gulls with specifically-programmed GPS data loggers at two German breeding colonies in May 2013 in order to study flight-height distributions during foraging. We hypothesize different flight heights for varying phases of foraging trips: (1) As lesser black-backed gulls use differing habitat types and structures for foraging we propose that heights would differ between flights over land and over sea. (2) During nocturnal foraging gulls are supposed to fly in lower heights than during diurnal foraging flights according to the worse lighting conditions. (3) For most seabird foraging trips commuting and tortuous phases can be identified. The latter are presumed to indicate active foraging while commuting flights between the single foraging spots might be rather straight and fast (e.g. Votier et al. 2010). Therefore and for orientation, we expect the gulls to fly higher during commuting flights than during active foraging. (4) We expect inbound flights back to the colony to be higher than outbound flights at the beginning of each trip, because birds might fly faster and straighter back to the colony after foraging to spell the mate at breeding.

Materials and Methods

Study design

Eleven adult lesser black-backed gulls were caught during incubation on the East Frisian Islands of Norderney (53°43'N, 7°18'E) and Juist (53°40'N, 7°04'E; Germany) using walk-in traps in 2013 (capture 15–21 May; recapture 1–8 June). All gulls were color-ringed and equipped with GPS data loggers (Earth & Ocean Technologies, Kiel, Germany; mass: 23 g including casing; dimensions: 46.5 mm × 32 mm × 18.5 mm). Birds were handled under a license issued by the National Park Administration of the Wadden Sea National Park of Lower Saxony, Germany and the Lower Saxony State Office for Consumer Protection and Food Safety, Germany (file number: 33.9-42502-04-11/0666). The data loggers were fixed at the base of the four innermost tail feathers using textile adhesive TESA® tape (Beiersdorf AG GmbH, Hamburg, Germany). The total attached mass of the devices was 26 g, i.e. 3.3% (range: 2.8–4.2%) (Kenward 2001, Phillips et al. 2003) of the average body mass of the captured lesser black-backed gulls (786 g; range: 609–976 g; n_{birds} = 10). The data loggers were left on the gulls for 2–16 days, due to the repeated use of four devices. Three birds could not be recaptured because of nest predation. Sex was not considered as a factor because of the small number of females. All birds were weighed at capture.

Flight heights

The data loggers recorded geographical position, instantaneous speed, flight direction, and flight height. Recorded flight height is not usually accurate enough to answer various biological questions (current accuracy is described as ±20 m) (Cook et al. 2012). The accuracy of flight-height measurement depends on the operating mode: the shorter the log interval, the more accurate the values (Thaxter et al. 2011). In order to maximize accuracy and battery life, we therefore programmed the loggers to record data continuously for 35 seconds, at 5-min intervals. This duration was selected based on previous trials (calibration height: 11 m above sea level; n = 5; ±1 m: 17%, ±5 m: 41%, ±10 m: 32%, ±15 m: 8%, ±20 m: 2%). Flight-height values ceased to change after 35 seconds, and the last value was used for analysis.

Statistical analysis

Only trip data were analyzed in the current study, i.e. nest attendances were excluded from further analyses. All trips heading out to sea or inland, with no previous resting near the colony, were defined as foraging trips. All data falling below an instantaneous speed of 10 km h^{-1} were assumed to indicate birds sitting, walking, or floating on water, according to

Shamoun-Baranes and van Loon (2006), and were therefore deleted. One flight-height measurement (at-sea position) of -67 m above sea level was treated as a measurement error and was therefore excluded from further analyses. Inclusion or exclusion of this outlier did not change the significance of any model.

Trip data were divided into land and sea positions using the geographical information system software ArcGIS® 10.0 (ESRI 2011). Hours from 22:00 to 04:49 Central European Summer Time (CEST) were classified as ‘night’, and hours from 05:00 to 21:59 CEST as ‘day’, according to the averaged sunrise and sunset times of the respective study days. Straight and tortuous flights were distinguished by splitting each trip into 30-min segments. The straightness index of each segment was calculated according to Benhamou (2004): the direct distance from start to end point was divided by the birds’ actually flown distance per each trip segment. The values of the straightness index range from 0 to 1 with high values indicating a straight flight path. Inbound and outbound flights from the breeding colonies were defined as the last and first 15 min of each trip, respectively.

All statistical analyses were performed using the open source software R 3.0.2 (R Development Core Team 2013). For model selection we applied Linear Mixed Models (LMM) (Faraway 2006) using the lmer function of the R package lme4 (Bates et al. 2013). LMMs based on the REML estimation were used to test for differences in flight height between flight destination (land/sea), time of day (night/day), flight type (straight/tortuous), and inbound and outbound flights from the breeding colony. Flight heights might also be influenced by distance of individuals from their nest (Alerstam et al. 1974; Kahlert et al. 2012), and this factor was therefore included in the model. Possible effects of weather conditions on flight heights (Liechti 2006) were accounted for by including wind direction and wind speed as additional predictors. Data were obtained from the meteorological station Norderney (53°42'43.92"N, 7°9'6.84"E; sensor height above ground: 11.8 m) of the German Weather Service (DWD, downloaded from http://www.dwd.de/webwerdis) for the whole study period. We calculated a tailwind component on the basis of hourly wind direction and wind speed values and modified the tailwind component of Akesson and Hedenström (2000) as $V_S \cos(\varphi_C - \varphi_W)$, where V_S is the wind speed, φ_C is the flight course of each gull and φ_W is the wind direction.

Flight height was used as the response variable, with the other above-mentioned traits as fixed effects. Inbound and outbound flights were tested separately because of different numbers of GPS fixes ($N_{fix} = 86$), while all other fixed effects were tested in a single model ($N_{fix} = 394$). Trip id nested within individual id were treated as random factors to avoid pseudoreplication. The significances of all fixed effects were tested by comparing each full model with the reduced model using ANOVA (χ^2 with one degree of freedom) (Faraway 2006). All non-significant effects were excluded from the end model via stepwise backward selection (end model predictors: flight destination, time of day, straightness index, inbound/outbound flights, distance to nest, tailwind component, and interaction between tailwind component × flight destination). To achieve normality, flight-height values were log-transformed. A Gaussian error distribution was used in all models. Because flight heights in two subsequent observations were not independent of each other, we accounted for temporal autocorrelation using the lme function in the nlme-package (Pinheiro et al. 2013).

Results

Flight heights

The flight heights of the eight tracked lesser black-backed gulls (Fig. 19) from which loggers were recovered during a total of 28 foraging trips (1–8 trips per individual) ranged from -10 to 723 m (N_{fix} = 394). Most GPS fixes (89%) represented heights below 20 m. The proportion of negative heights was about 1%. Altitudes above 100 m were rarely recorded (ca. 1% of records).

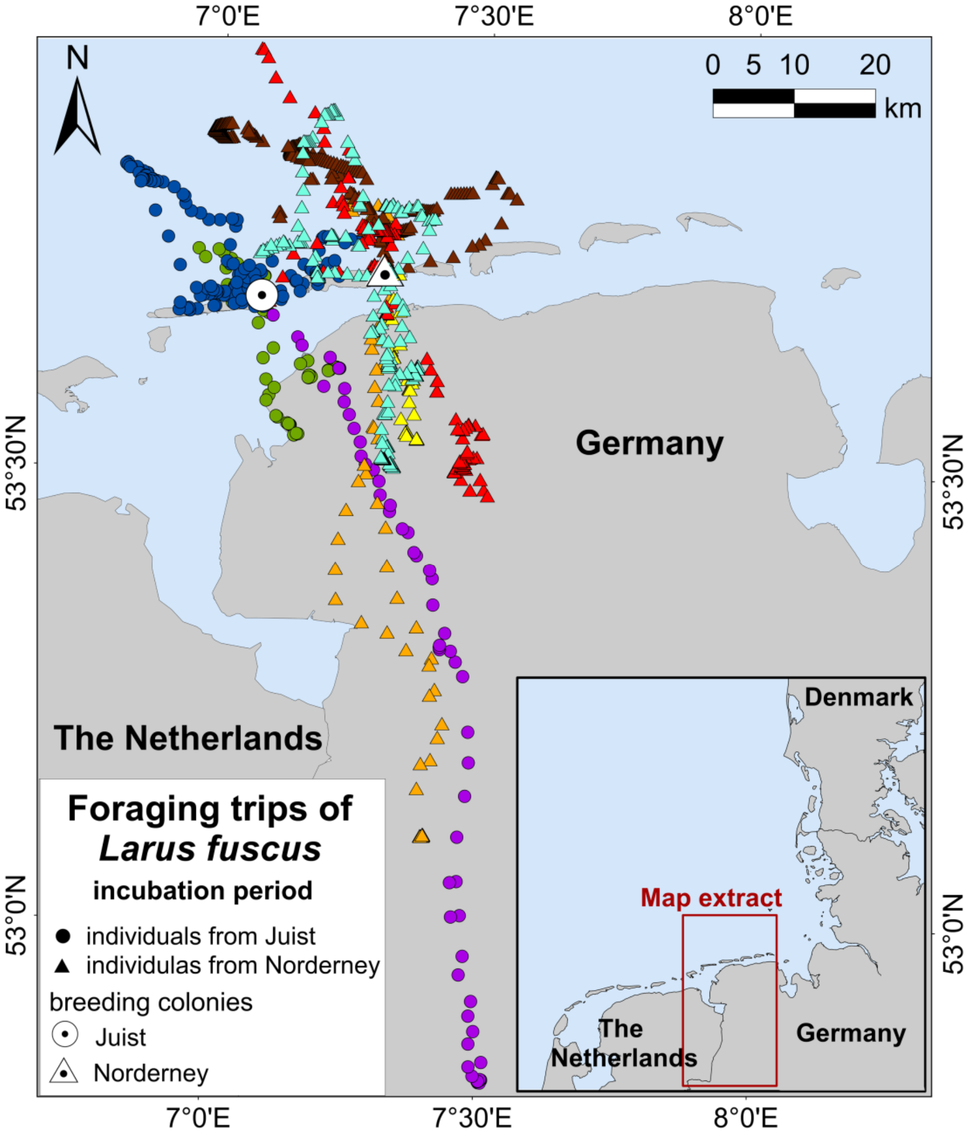

Fig. 19 Foraging trips of lesser black-backed gulls from Juist and Norderney during the incubation period, 2013

Flight heights differed significantly between flight destinations, times of day, and flight types (Fig. 20): gulls flew higher over land (25%-quartile: 10 m, 75%-quartile: 43 m) than at sea (25%-quartile: -1 m, 75%-quartile: 8 m; LMM, t = 3.1824, *P* = 0.0016, df = 360) and lower at night (25%-quartile: -2 m, 75%-quartile: 8 m) than during the day (25%-quartile: 2 m, 75%-quartile: 35.5 m; LMM, t = -2.4619, *P* = 0.0143, df = 360). Gulls also flew higher during straight flight segments than during tortuous movements (LMM, t = 2.8031, *P* = 0.0053, df = 360)). Outbound and inbound flights were performed at similar heights (LMM, t = -1.371, *P* = 0.1764, df = 51). Flight height increased with increasing distance from the nest (LMM, t = 5.5339, *P* < 0.0001, df = 360). Neither the tailwind component nor its interaction with flight destination affected the flight height (all *P*-values > 0.12).

In terms of the course of each individual foraging trip, birds appeared to fly at higher altitudes after completed 40–60% of their trip (Fig. 21).

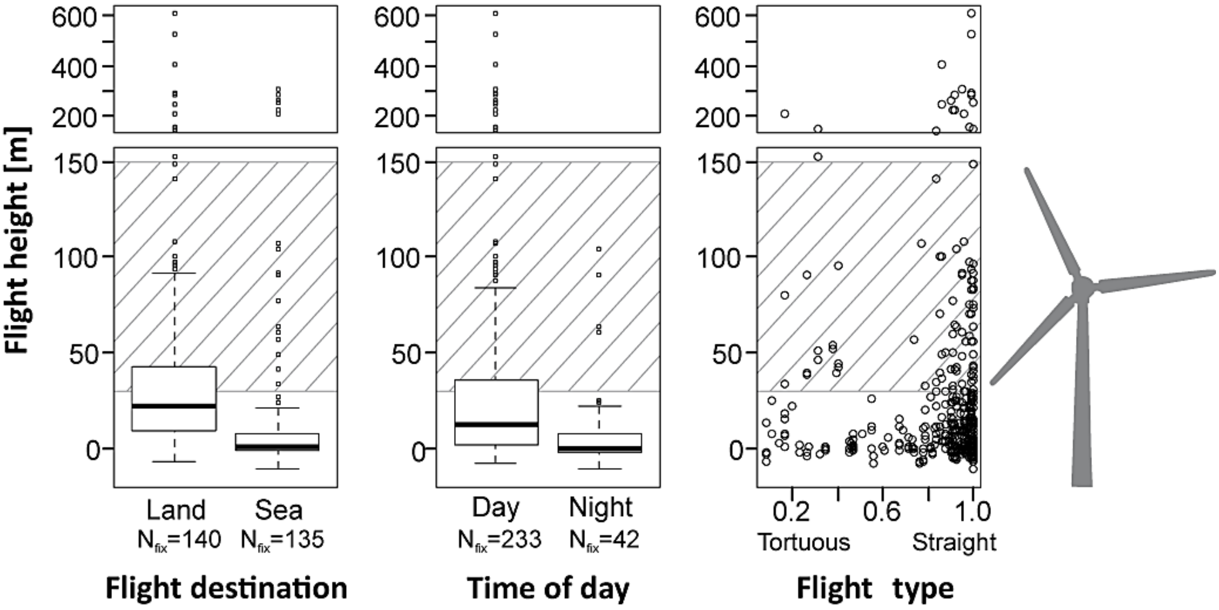

Fig. 20 Flight heights of lesser black-backed gulls during flights over land and at sea (*flight destination*), at day and at night (*time of day*) and during tortuous and straight movements (*flight type*). Gray shaded areas indicate the rotor area of most operating offshore wind turbines. Boxes represent 50% of the data between the first (25%) and the third (75%) quartile. Upper and lower whiskers represent 25% of the remaining data, respectively. The median is represented by the horizontal black line

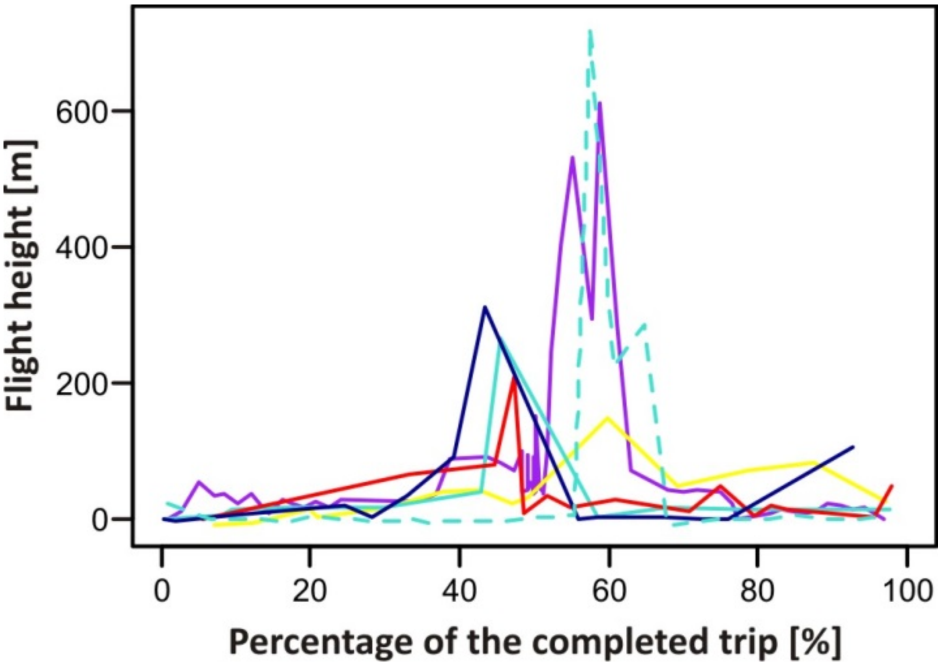

Fig. 21 Flight heights of selected lesser black-backed gulls (n_{birds} = 5, n_{trips} = 6) during single trips. Different colors indicate different individuals according to Fig 1; different line types indicate different foraging trips by the same individual

Discussion

Instrumentation effects

We used recommended streamlined data loggers with a total attachment mass of 3.3% of the average body mass of the birds (Kenward 2001). Comparison of the body mass of the equipped gulls (n_{birds} = 5) at capture (mean ± sd: 881.4 ± 72.5) and recapture (mean ± sd: 822.0 ± 58.9) indicated an average body mass loss of 59.4 g (6.7%), although this body mass loss was not significant (t-test, t = 1.4, df = 7.7, P = 0.2). Four individuals lost (range: 0.9–14.0%) and one gained body mass (3.7%). Three of 11 gulls lost their clutches as a result of predation. We confirmed chick hatching in the remaining eight individuals. We were unable to conduct detailed behavioral observations of unequipped individuals, but we monitored the behavior of caught individuals after release. Most of the captured birds initially left the colony, but returned after 5–10 min to continue incubating. We detected no abnormal behavior during observations of the equipped individuals throughout the capture period. One of the equipped birds from Juist was subsequently recovered in Lincolnshire, United Kingdom, at the end of July 2013. We therefore considered the effects of the instrumentation on the gulls to be low, though it was impossible to exclude behavioral and energetic impacts completely.

Flight heights

Lesser black-backed gulls flew at variable heights, though most recorded flights were below 20 m. This is in accordance with the results of other studies (Garthe and Hüppop 2004;

Mendel et al. 2014). Shamoun-Baranes and van Loon (2006) conducted radar measurements on an inland airbase in the southeastern Netherlands and found mean flight heights of 175 and 298 m for flapping and soaring flights, respectively. However, they concentrated on gulls moving to or from their foraging grounds within a range of 5 km, and thus only investigated a small percentage of all foraging trips, making their recorded heights not comparable with those in the current study. Lower flying at sea compared with over land might be explained by the gulls' opportunistic foraging behaviour: food availability at sea is more unpredictable than on land, and the gulls may take advantage of rapidly-available food by flying near to the sea surface. In contrast, when foraging on land, the gulls may search for a suitable site by flying high enough to gain an overview for orientation, and then subsequently follow their prey on foot. Another advantage of flying near sea level is that it minimizes energy expenditure by avoiding strong winds at greater heights and due to the ground effect (Withers and Timko 1977). Furthermore, there are fewer obstacles to avoid at sea compared with in land habitats.

Foraging trips during the day might be conducted at higher altitudes than those at night because of better visibility; lesser black-backed gulls are visual predators (Glutz von Blotzheim and Bauer 1982) and thus depend on light. However, they often scavenge behind fishing vessels at night (Camphuysen 1995; Garthe and Hüppop 1996), if there is sufficient light, and this could also be relevant on land e.g. at artificially-illuminated meat-processing factories, suggesting that lesser black-backed gulls might depend largely on anthropogenic food sources at night. In the current study, most of the nocturnally-foraging gulls flew at sea. Tagged birds also flew higher during straight flights compared with tortuous flights. Straight flights represented commuting between different foraging sites and/or the breeding colony, while tortuous flights mostly indicated active foraging (Votier et al. 2010), which requires a low height to permit the rapid capture of prey.

Contrary to expectations, flights out of and into the colony were performed at similar heights. One explanation for this could be that lesser black-backed gulls already know their foraging target when starting a trip, and therefore do not need to fly high in order to orientate themselves. Furthermore, both outbound and inbound flights were relatively straight, rather than tortuous. However, a shorter recording interval is needed for a more detailed analysis of the straightness of outbound and inbound flights, given that they only represent the first and last 15 min of each trip.

The extreme heights observed in most tagged individuals after about half the total trip time might indicate an orientation phase; they might have finished foraging and need to orientate for the flight back home, or might be searching for the next foraging site. A further study with a larger sample size is needed to study this pattern in more detail.

The apparent absence of any effect of wind on flight height might be associated with the large-scale resolution of the wind-measurement data, which did not accurately reflect the conditions along the gulls' flight paths. We did not account for the increase of wind speed with increasing altitudes following e.g. Bañuelos-Ruedas et al. (2010), because the vast majority of fixes represent heights below 20 m.

Conclusions

Foraging lesser black-backed gulls vary their flight heights according to their destination, time of day, and flight type. Detailed knowledge of flight-height distributions is important in terms of understanding flight energetics and foraging behavior, but is also essential for making adequate impact assessments of the effects of both offshore and inland wind farms on birds' flight and foraging patterns. Most GPS fixes were recorded at heights below 20 m, indicating an overlap, and thus a potential collision risk, with operational rotor heights. Despite its limitation to relatively small numbers of birds, the use of GPS data loggers to track individual flight heights might prove a useful tool for developing a comprehensive understanding of avian flight heights, especially during foraging, both inside and outside of wind farms.

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CHAPTER IV:
Marine wind farms, fisheries and northern gannets: a pilot study in the southern North Sea

Garthe S, Corman AM (submitted) Marine wind farms, fisheries and northern gannets: a pilot study in the southern North Sea

Marine wind farms, fisheries and northern gannets: a pilot study in the southern North Sea

Stefan Garthe and Anna-Marie Corman

Abstract

We studied the distribution of northern gannets – a species of high conservation concern – in the southern North Sea in relation to fisheries and offshore wind farms.

The distribution was derived from ship-based and aerial surveys following standardised transect counts, while individual chick-rearing adults from the breeding colony on Helgoland were tagged with GPS data loggers.

Gannets were distributed throughout most of the German Bight, with a core area to the west of Helgoland. A few long foraging trips led to areas west of Jutland in Denmark. Foraging trips of tagged gannets lasted from 0.4 to 53.5 h, total distance flown per foraging trip ranged from 4.7 to 937.9 km and foraging range varied between 2.0 and 320.8 km. Only 0.9 % of counted gannets were associated with fishing vessels. Gannets largely avoided the wind farm area north of Helgoland. One individual crossed a single wind farm four times, but at that time turbines were not installed yet.

The clear avoidance of wind farms implies that gannets may not suffer from mortality due to operating rotor blades, but that they may experience substantial habitat loss instead. GPS tracking is well-suited to study wind farm effects and possible habituation processes at the individual level, which is important considering the massive plans for offshore wind farm constructions in the North Sea.

Keywords: environmental impact assessment, foraging patterns, fisheries, habitat loss, *Morus bassanus*, offshore wind farms

Introduction

Concerns about risks for birds at offshore wind farms are intensifying as developments have expanded widely in coastal and offshore marine environments (Garthe and Hüppop 2004, Furness et al. 2013). Current plans in the North Sea involve several thousand wind turbines with similar plans emerging in the western Atlantic, other European areas and throughout the world. Calls for renewable energy plans are intensifying by political and societal desires for "green" energy and concerns about the Fukushima Nuclear Power Plant leakage in Japan during March 2011 and the Gulf of Mexico oil disaster in April 2010.

Assessing potential risks associated with proposed wind energy installations is essential. Enhancement of environmental assessment information and approach is a critical concern, because recent evaluation has found a weak relationship between environmental impact assessment predictions and subsequent avian mortality at wind energy installations (Ferrer et al. 2012).

Experiences from operating wind farms are limited. Lindeboom et al. (2011) infer from detailed observations of a wind farm in the southern North Sea that, overall, the wind farm creates a new type of habitat involving an artificial reef (e.g. Bohnsack et al. 1994), with a high biodiversity of benthic organisms, and increased use of the area by fishes, marine mammals and some bird species as well as a decreased use of the area by other bird species.

Seabirds can be generally affected by offshore wind farms in four ways (Dierschke and Garthe 2006): 1) collisions; 2) barrier effects that could cause birds to avoid a wind farm by flying around it (horizontal escape), under or over it (vertical escape) that could in turn increase energy and possibly stress costs; 3) habitat loss by displacement due to disturbance by operating turbines and associated ship and helicopter traffic; 4) attraction by increased food availability due to creation of hard-bottom substrate at turbine bases and to fishing bans near sites.

To study possible effects of existing wind farms on seabirds, we performed a pilot study in the southern North Sea in 2014. We selected the northern gannet (*Morus bassanus*; thereafter gannet) as target species as it is ranked among those of highest overall risk as related to offshore wind farms in the UK, where the largest breeding sites exist (Langston 2010). Also, gannets are well-suited for deploying high-resolution data loggers to study their flight paths, distributions and foraging ecology (e.g. Garthe et al. 2007, Soanes et al. 2013). In addition to tagging birds on the breeding colony of Helgoland, we also analysed long-term seabirds at sea data to obtain information from a very comprehensive data set. Furthermore, we also analysed the extent to which gannets were associated with fishing vessels. While fishing boats are known to influence the foraging trips of gannets by providing food at regular intervals (Votier et al. 2010), fishing vessels are likely banned from wind farm areas (e.g. Bergman et al. 2015), so that the location of fish trawlers may change and in consequence also the distribution of scavenging seabirds.

Material and Methods

Study area

This study took place in the southern North Sea, Europe. The island of Helgoland (54° 11' N, 7° 55' E), Germany, holds the only gannet colony in this part of the North Sea. Data on numbers of breeding gannets were summarized for this study.

Data logger study

Seven chick-rearing adults were caught on 04 July 2014 and equipped with GPS data loggers ('Bird Solar', e-obs GmbH, Munich, Germany; 'CatLog-S GPS', Catnip Technologies, Hong Kong, China). Loggers were attached to the base of the four innermost tail feathers using TESA® tape (Beiersdorf AG GmbH, Hamburg, Germany). From 08 to 10 August, all birds were resighted, with their chicks being in good condition. Data from three birds could be retrieved through remote-reading from 08 to 10 August 2014 and/or by recapturing the birds on 11 September 2014. One device malfunctioned, two more were lost to on-going tail-feather moult and one device could not be retrieved as the chick was fledged at recapture. Total data sets for this study were thus three birds, tracked for 69, 37 and 24 days, respectively.

Total attachment mass of the devices (including sealing, base plate and tape) was ca. 56 g ('Bird Solar') and 39 g ('CatLog-S') representing 1.7% and 1.2%, respectively, of the mean body mass of 3,286 g (Wanless and Okill 1994) and thus clearly below a potential threshold of 3% (Phillips et al. 2003, but see Vandenabeele et al. 2012). Attachments on the tail may negatively influence the flight behaviour of the birds (Vandenabeele et al. 2014), but all pairs successfully raised their chick and no visual effect on the bird could be detected.

Seabirds at sea study

To study the background scenario, the distribution of gannets was derived from ship-based and aerial surveys following standardised transect counts (Camphuysen et al. 2004; Markones and Garthe 2012). A comparative study of seabird surveys in German waters revealed that densities of gannets were equally well assessed from both counting platforms (Markones and Garthe 2012) so that data from ship-based and aerial surveys were combined in this study. Densities were derived using the distance sampling methodology (Buckland et al. 2001) by calculating correction factors for birds increasingly overlooked in the outer transect bands.

We analysed data from June to September during 2005–2012. In total, effort comprised 21,799 km of ship-based surveys and 41,593 km of aerial surveys. Data from before 2013 were selected to represent a situation nearly without wind farms: only two wind farms were built since 2008 (first turbines in 2009) and 2010 (first turbines in 2012), respectively. Also, the growing gannet colony on Helgoland has to be taken into account for abundance estimates. Therefore; we only selected data from 2005 onwards, when the population comprised ≥200 pairs (Fig. 22). Most pairs were having chicks from June to September.

To interpolate distributional data from at-sea surveys, we rasterized the total number of gannets and the mapping effort (grid: 1km × 1km) and calculated the average abundance (number of gannets/transect km) per grid cell using ArcGIS 10.0 (ESRI 2011; equal-area projection: UTM). The rasterized data were spatially interpolated using a generalized additive model (GAM; Wood 2006) to identify the areas of main occurrence. All GAMs were conducted using R 3.0.0 (R Development Core Team 2014; R package mgcv; smoothing function: thin plate regression splines; Wood 2003, 2006). Gannet abundances were logarithmized to achieve normality. We used a quasipoisson distribution to account for the abundance values derived from our count data. The results of all models were visualised exluding areas which lay too far from the original data (function ‘vis.gam‘, Wood 2006; too.far = 0.05). Thus, areas with insufficient mapping effort and consequently higher uncertainty were excluded from the analysis. For visualization, coastline and wind farm shapes were intersected with the model output (R packages maptools, rgdal). Finally, the rasterized mapping effort was added.

The extent to which gannets attend fishing vessels may influence their distribution (Bodey et al. 2014a). To assess the relative importance of fishing boats, two methods were applied. First, the proportion of all gannets that were associated with fishing vessels were derived from ship-based seabirds at sea counts within the wider German Bight (east of 5°E, south of 56°N); this data set is based on 21,799 km of transects sailed between June and September 2005–2013. Second, fishing boats encountered during routine seabirds at sea counts were regularly scanned for ship-followers, if conditions allowed even at several km distance from the observation platform. For the same period and area, a total of 542 counts of ship-followers could be analysed, mainly comprising shrimpers and beamers, reflecting the typical fishing fleets in the German Bight (Fock 2008).

Status of offshore wind farms

Information on the location and status of wind farms in the study area were collated from the BSH (pers. comm.) and from the 'Global Offshore Wind Farms Database' (http://www.4coffshore.com/offshorewind/).

Results

The breeding colony on Helgoland

Helgoland was first established as a breeding colony for gannets in 1991 with the first pair breeding. Gannets continued to breed on Helgoland in the years following, while numbers strongly increased towards the end of the century. This increase continued almost consistently, with a current maximum of 656 nest sites in 2014 (Fig. 22).

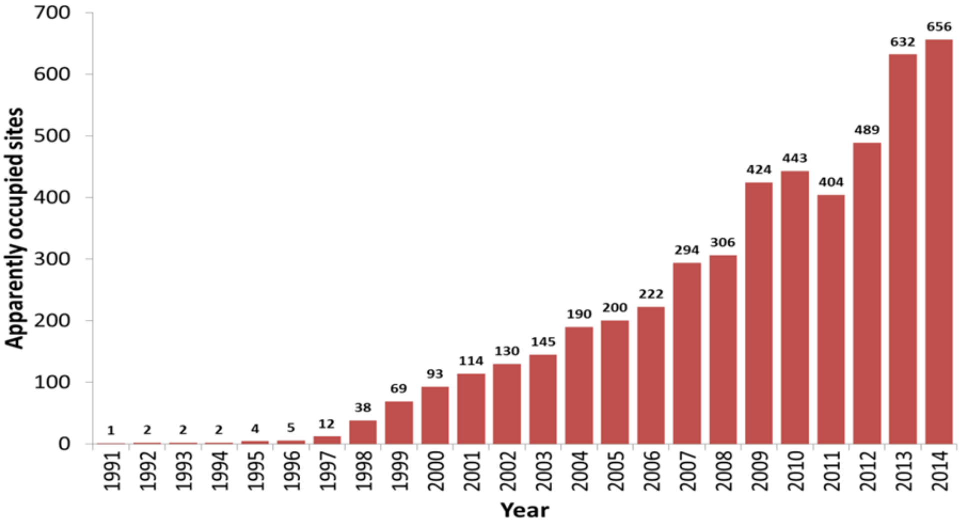

Fig. 22 Population trend of northern gannets on Helgoland, southern North Sea (source: Institute of Avian Research, O. Hüppop and J. Dierschke, pers. comm.)

General distribution

The distribution of adult gannets extended throughout most of the German Bight, but the core area of birds counted at sea was to the west of the island (Fig. 23). A further hotspot was visible far in the west and apparently not linked to Helgoland.

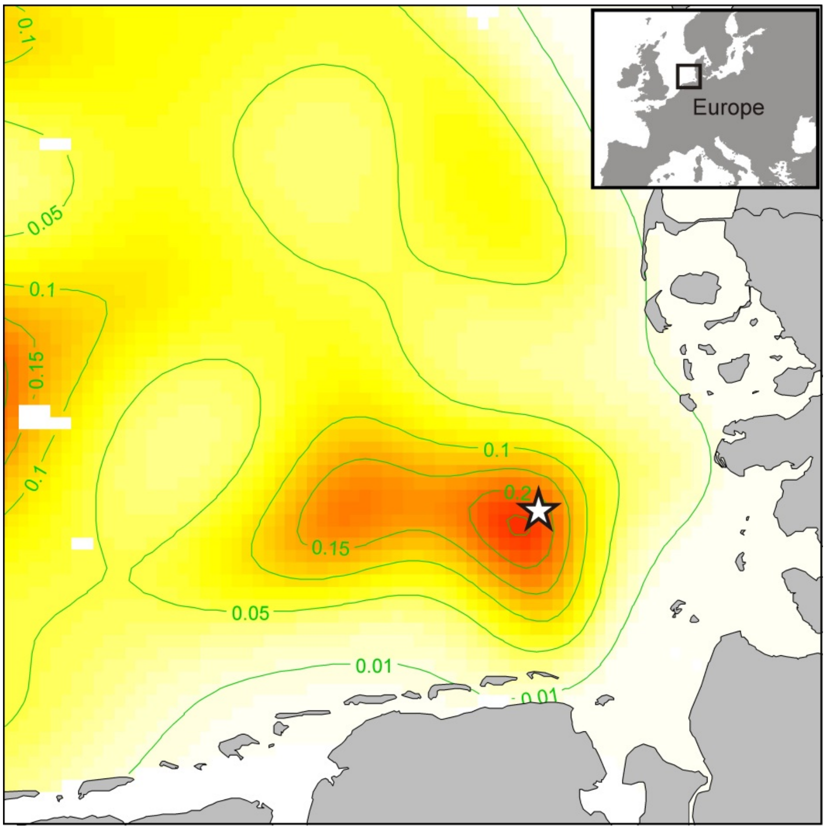

Fig. 23 Distribution of northern gannets from ship-based and aerial seabirds at sea counts, 2005-2012. Increasing gannet densities are visualised by colours from yellow through orange to red. Green contours and numbers represent the abundance (no. birds/mapping effort) of gannets. The white star represents the location of the breeding colony

The flight tracks of the three adult birds tagged showed the highest density of positions at sea to the west of the island, but also to the south and a marked axis to the northwest of Helgoland (Fig. 24). A few long foraging trips led to areas west of Jutland in Denmark, while there were no trips directed far to the west.

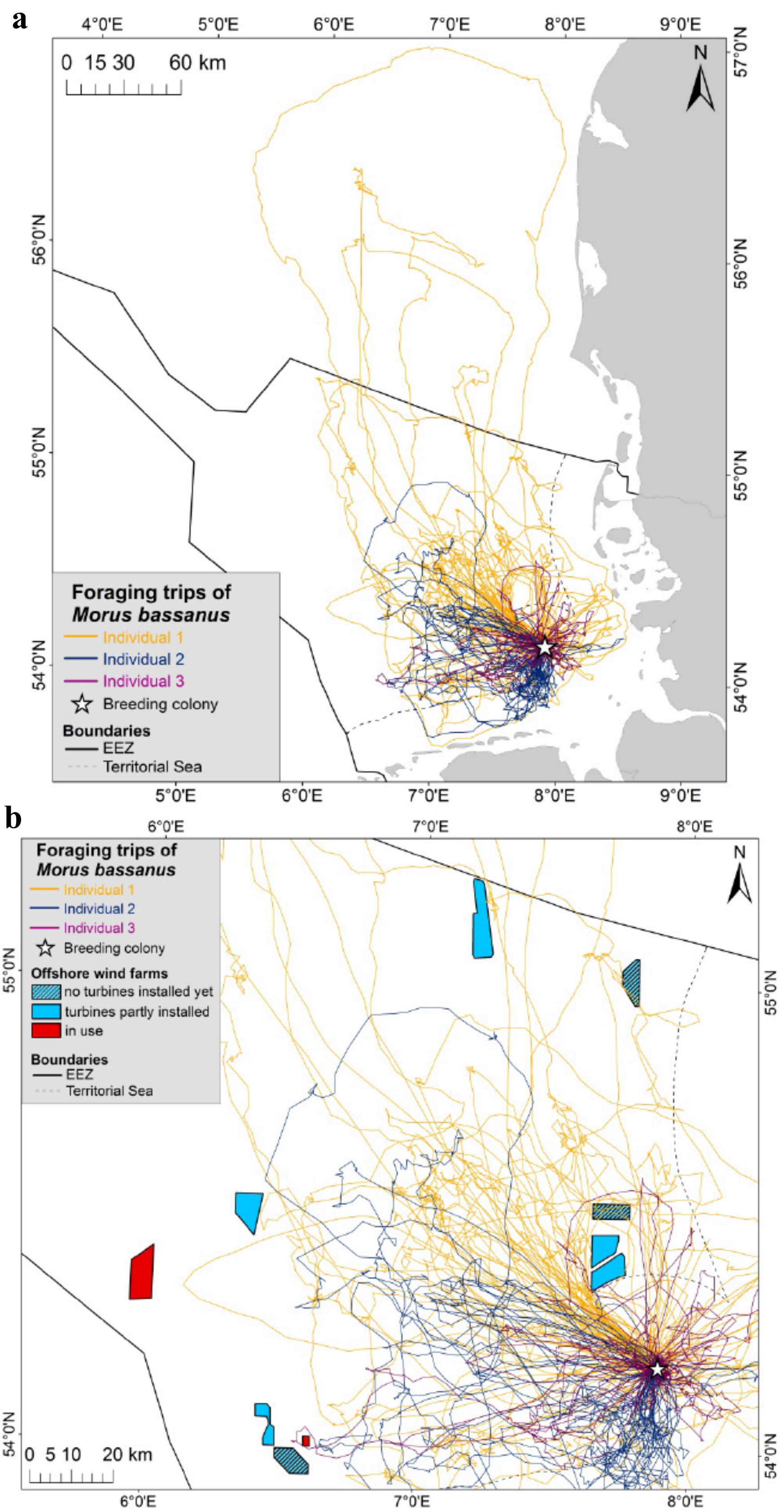

Fig. 24 Flight tracks of three northern gannets breeding on Helgoland, Germany, over 4, 5 and 9 weeks, respectively, from early July 2014 onwards. **a** Complete flight tracks, **b** overlap with marine wind farm areas

Foraging trips of birds breeding on Helgoland

Foraging trips of gannets from Helgoland lasted from 0.4 to 53.5 h, with an average of 7.9 ± 8.0 h (n_{trips} = 168, n_{birds} =3). Averages of individuals varied between 6.9 h and 8.6 h. Split into 3 periods (the first 2 being shorter to get a better coverage of the different individuals), foraging trips lasted on average 7.2 h from 04 to 23 July (n_{trips} = 84, n_{birds} = 3), 7.9 h from 24 July to 12 August (n_{trips} = 49, n_{birds} = 3) and 9.5 h from 13 August to 10 September (n_{trips} = 35, n_{birds} = 1).

Total distance flown per foraging trip ranged from 4.7 to 937.9 km. The overall mean ± SD was 124.6 ± 138.6 km (n_{trips} = 168, n_{birds} =3), individual means varied between 70.7 and 146.1 km. Total distance flown was on average 95 km from 04 to 23 July (n_{trips} = 84, n_{bird} = 3), 138 km from 24 July to 12 August (n_{trips} = 49, n_{bird} = 3) and 178 km from 13 August to 10 September (n_{trips} = 35, n_{bird} = 1).

The averaged foraging range of gannets was 42.0 ± 45.7 km, with extreme values ranging from 2.0 to 320.8 km (n_{trips} = 168, n_{bird} = 3). Individual means were found to lay between 23.8 and 51.4 km. Foraging ranges amounted on average to 32 km from 04 to 23 July (n_{trips} = 84, n_{bird} = 3), 42 km from 24 July to 12 August (n_{trips} = 49, n_{birds} = 3) and 67 km from 13 August to 10 September (n_{trips} = 35, n_{bird} = 1).

Association with fishing vessels

During routine ship-based seabirds at sea counts, only 19 out of a total of 2,042 gannets (= 0.9 %) were found to be associated with fishing vessels while recorded. Of the 542 scans of ship-followers at fishing boats, only in two cases (0.4 %) gannets were recorded as followers, once a single bird and once ten birds.

Overlap of gannet distribution with marine wind farms

The flight tracks (Fig. 24a) revealed a gap of tracks to the NNW of Helgoland. Projecting the wind farm sites onto the map showed that the birds most obviously avoided that wind farm area (Fig. 24b). Although all individuals apparently approached wind farm sites at least a few times during their trips, only one individual flew through the northernmost of the three wind farms located north of Helgoland. The bird crossed the site four times, but at this time only a transformer station and a platform as well as the foundations were installed, while turbines were not installed until February 2015.

Discussion

This study clearly shows that gannets use wide areas of the German Bight, with a concentration on areas to the west and northwest of the breeding colony. Data also demonstrate that gannets are rare scavengers in the German Bight and are thus likely not influenced by the distribution of the different fishing fleets operating in this intensively used fishing area (Fock 2008). The low rate of attending fishing vessels is a remarkable difference to gannet colonies in the UK where gannets are known to extensively use this additional food source (e.g. Votier et al. 2010). The small size of the colony, the distance of more than 500 km to the next colony and the comparatively short distances and durations of the foraging trips suggest that intraspecific competition at Helgoland is low (Wakefield et al. 2013); maybe there is simply no need to prey on discards that are furthermore much lower in energy density than pelagic fish species (Garthe et al. 1996).

Focusing on the offshore wind farms, the three individuals tagged over several weeks showed clear avoidance of those areas where turbines were installed. Seabird distribution prior to turbine installation showed that these areas were visited in the same intensity as other nearby areas. Nevertheless, all wind farms were approached by gannets and sometimes surrounded. Though the sample size was rather low in this pilot study, the results match well studies at operating wind farms that found in most but not all cases (e.g. Gill et al. 2008) that at least during good visibility gannets strongly avoided wind farms, with most birds changing their flight trajectories when approaching the site (Petersen et al. 2006; Krijgsveld et al. 2011).

This behaviour has two implications for gannets: First, when they avoid wind farms, they may not suffer from mortality in these wind farms (Rothery et al. 2009). Though gannets usually fly at low altitudes (Johnston et al. 2013), below the minimum height of any turbine rotor blades, they sometimes reached altitudes up to 50 m or even more when searching for food (Krijgsveld et al. 2011; Garthe et al. 2014), putting them at risk to collide with the rotor blades. Second, when gannets are totally or partially displaced from wind farm areas, they may experience habitat loss. This might not be problematic as long as only a few wind farms are established. With an increasing number of wind farms effects may add up and may eventually pose a considerable impact on the species (e.g. Busch et al. 2014; Leopold et al. 2014). This may not only relate to the wind farm area itself but possibly also to buffer zones (Dierschke et al. 2006) as well as to "wake zones" on both sides of the wind farms, especially if birds are commuting to and from a colony.

This study combines different methods to study gannet distribution and behaviour. While seabirds at sea data and observations on birds attending fishing vessels give very relevant baseline data, visual surveys for birds are considered unlikely to have enough power to detect changes in behaviour or fine scale spatial or temporal shifts in distribution (Bailey et al. 2014). Instead, techniques such as GPS tracking, radar, and fixed cameras are likely to provide more useful data for seabirds (Bailey et al. 2014). Indeed, tracking data of foraging seabirds provide a useful tool for gaining such data at operating wind farms (Thaxter et al. 2015). This methodology is also well-suited to study wind farm effects and possible habituation processes at the individual level. Repeated tracking of the same individuals may help identifying changes in birds' responses over time to existing wind farms. This is particularly interesting for breeding birds that may learn about these wind farms over long exposure time – in contrast to migrating birds that usually encounter the same wind farm sites only once, twice or very few times per year. Considering the massive plans for offshore wind farms to be realised in the distribution area of gannets, it is of huge conservation importance to study comprehensively the species' responses and the risks involved.

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FINAL DISCUSSION

The current thesis provides detailed knowledge of the foraging ecology of lesser black-backed gulls and northern gannets breeding in the southern North Sea. It demonstrates that spatial segregation occurs on the population (chapter I), the sex-specific as well as the individual level (chapter II), and simultaneously highlights the importance of the level, on which the spatiotemporal foraging behaviour is considered (chapters I + II). High-precision data on flight and foraging patterns of seabirds, such as collected and analysed in this thesis, can also be used for impact assessments of anthropogenic exploitation of the sea (e.g. Bodey et al. 2014b; Thaxter et al. 2015), for environmental monitoring (e.g. Asseburg et al. 2006; Burger and Shaffer 2008), or consequently for conservation and management implications of the relevant species (Bograd et al. 2010; Camphuysen et al. 2012; Ronconi et al. 2012; Bogdanova et al. 2014). Furthermore, this thesis contains one of the first studies examining the vertical habitat use of a common seabird species via GPS telemetry (chapter III). Detailed knowledge of the vertical space use of birds provides an important basis for direct assessments of the collision risk with offshore wind farms (e.g. Cook et al. 2012; Johnston et al. 2013). Recently, there is an increasing number of tracking studies examining the impact of offshore wind farms on the individual foraging behaviour of seabirds (Bogdanova et al. 2014; Wade et al. 2014; Thaxter et al. 2015). Nevertheless, empirical tracking data on actual effects of already operating offshore wind farms are still scarce for most species (see Kaldellis and Zafirakis 2011 for a reviewed status quo of EU offshore wind farms), and impact assessments are rather available for proposed wind farm areas (e.g. Langston et al. 2013). This is most likely due to the delay in the practical implementation of offshore wind farms in most EU countries (Breton and Moe 2009; Snyder and Kaiser 2009; Haggett and Futak-Campbell 2011), especially in Germany (Gee 2010). Thus, the current thesis provides valuable data on the foraging patterns of breeding northern gannets and their behavioural reactions to operating wind farms (chapter IV).

Hereafter, all key findings, which are not discussed within the specific chapters of the current thesis, and their general applications will be considered in a broader context. In particular, the following aspects will be examined in detail:

- Occurrence of spatial segregation during foraging flights: what is more important in foraging seabirds, the consideration at the population or the individual level?
- How will seabirds cope with increasing anthropogenic pressures such as offshore wind farms?
- Future perspectives of studying lesser black-backed gulls and northern gannets.

Spatial segregation of foraging patterns at different levels

In ecological studies, foraging patterns can be analysed at different levels of consideration. Several studies considered foraging behaviour of marine predators at the population level (e.g. Furness and Birkhead 1984; Lewis et al. 2001; Robson et al. 2004). Recently, this approach is particularly used in tracking studies (Wakefield et al. 2013; Bogdanova et al. 2014; Ceia et al. 2014a). A large number of studies investigated the sex-specific foraging behaviours of seabirds (e.g. Weimerskirch et al. 2000; Lewis et al. 2002; Ludynia et al. 2013), i.e. at the next lower level of consideration. Currently, studies reporting the importance of individual foraging specialisation are increasing (Ratcliffe et al. 2013; Sommerfeld et al. 2013; Ceia et al. 2014b; Patrick et al. 2014). The most obvious question thus might be which approach is more important for the analysis of seabird foraging behaviour? The multi-colony approach, in which each colony can be seen as random sample of the population (as applied in this thesis), enables inferences and predictions for the whole geographic population of the respective study species. In particular, this approach is used for ecological impact assessments (e.g. Suter et al. 2005; Clutton-Brock and Sheldon 2010), and might serve as an early-warning system for population declines and consequently shifts in marine prey availability (Lewis et al. 2006; Bost et al. 2008; Elliott et al. 2008; Bodey et al. 2014b). Moreover, predictions can be made for future scenarios. For instance, how will the population react to environmental changes and to increasing anthropogenic pressures at sea such as the upcoming fish discard ban of the EU? Simultaneously, sex-specific and individual variations or specialisations may be masked, when considering colony-specific foraging patterns only (Bolnick et al. 2003; Ratcliffe et al. 2013; Sommerfeld et al. 2013).

In case of the lesser black-backed gull, spatially segregated foraging patterns occur at the population, the sex-specific and the individual level. The latter, however, was not explicitly tested, but strongly indicated during analyses (chapters I + II). In contrast to the apparent spatial segregation, trophic segregation in lesser black-backed gulls is less important at the colony level, but appeared at the sex-specific level. However, it cannot be exclusively attributed to the sexes, as analyses indicate a large between-individual variation, and consequently a high amount of individual specialisation. Thus, this species shows a multi-level strategy to avoid intra-specific competition. Individual specialisation in foraging lesser black-backed gulls seems to be large, but further studies are needed to analyse its role within the different levels of consideration, and interactions with intrinsic (e.g. body condition) and environmental factors.

Impacts of offshore wind farms on seabird foraging behaviour

Detailed knowledge of seabird habitat utilisation is crucial for any impact assessment on the birds' foraging behaviour. Studies assessing the impact of offshore wind farms on seabirds are mostly based on aerial or boat surveys and radar measurements at the specific wind farm areas (Camphuysen et al. 2004; Desholm and Kahlert 2005; Maclean et al. 2009; Fox et al. 2006).

Monitoring data cannot reliably assign the observed birds to any breeding population, and only represent a snapshot during each survey. Radar measurements have difficulties with identifying the species connecting to wind farm areas, and are somehow spatially restricted to the relevant wind farm they are built at (Desholm et al. 2004; Walls et al. 2009; Thaxter et al. 2011). In contrast, telemetry data of foraging seabirds offer an individual and permanent tracking of birds from a known breeding site around, within and between offshore wind farms (Langston et al. 2013; Wade et al. 2014; Thaxter et al. 2015). Thus, the GPS telemetry provides another useful tool for gaining data on possible impacts of wind farms on birds, though it might be limited regarding the number of equipped individuals.

Although the construction of offshore wind farms currently lags behind the schedule (e.g. Suter et al. 2005), there will be a large offshore area occupied with wind farms in the near future. That is of particular importance for relatively wide-ranging species like northern gannets. The clear avoidance of such wind farm areas by this species will mean a huge loss of foraging habitat, if this behaviour is corroborated in the following years. They will thus not only need to switch to other foraging sites, but will also be constrained to predefined commuting routes to reach suitable sites. If gannets, however, fly into the wind farm areas occasionally, the increasing collision risk accompanied with the increasing number of offshore wind farms will further complicate the situation.

Detours the birds have to fly in avoidance of offshore wind farms along their foraging trips are known to produce flight costs possibly leading to reduced body condition of adults and/or chicks (Masden et al. 2010). According to Masden et al. (2010), this additional energy expenditure depends on the specific wing loading, the flight mode (e.g. Pennycuick 2008; Masden et al. 2010), and on the environmental conditions of the relevant study year (Hamer et al. 1993; Pettex et al. 2012; Thaxter et al. 2015). The additional energetic costs for northern gannets and lesser black-backed gulls are estimated to be low due to their efficient gliding flight and their low wing loading (Masden et al. 2010).

There is evidence for some other seabird species which respond to operating wind farms by switching to areas without wind farms nearby. For instance, Mendel et al. (2014) found that common guillemots (*Uria aalge*) and divers (*Gavia* spp.) clearly avoided the studied wind farm area and their close surroundings for several years. However, the wind farm considered in this study only comprised twelve turbines, i.e. was small compared to all other approved projects in the North Sea. Nevertheless, birds may habituate or may be forced to habituate to the wind farms due to the ongoing habitat loss or due to changes in prey distribution (Dierschke and Garthe 2006; Dierschke et al. 2006). So, it is possible that areas that are avoided first may be used for commuting or foraging after a certain time period, but studies examining the habituation effect of seabirds to offshore turbines are still very scarce (e.g. Dierschke and Garthe 2006; Leonhard et al. 2013).

To assess the cumulative impacts of all constructed wind farms, further studies are needed (e.g. Busch et al. 2013; Leopold et al. 2014). Moreover, there is an urgent need for e.g. quantified avoidance rates and collision risks seabirds are exposed to. In addition, long-term studies over several years and throughout the annual cycle accounting for annual, seasonal as well as individual variation of seabird foraging behaviour are recommended (Bogdanova et al. 2014; Thaxter et al. 2015). The focus thereby should be on horizontal and vertical flight patterns of seabirds in time and space.

Future perspectives

The findings of this thesis contribute to fill knowledge gaps in seabird foraging ecology. Nevertheless, several questions remain unanswered.

Primarily, this thesis only covers the incubation period and not the whole breeding season (due to limitations of the devices used on lesser black-backed gulls), which is highly demanding concerning certain restriction to the clutch. The subsequent chick-rearing period is even more demanding, because both parents have to balance chick and self-provisioning simultaneously. Recent advances in miniaturisation of solar-powered GPS data loggers (e.g. Bouten et al. 2013) enable the attachment of species like lesser black-backed gulls, and increasingly lighter species, and thus make it possible to record individuals throughout the whole annual cycle. Therefore, it will be possible to analyse carry-over effects from different life history stages to breeding (Sorensen et al. 2009; O'Connor et al. 2014; Salton et al. 2015) or vice versa (e.g. Catry et al. 2013). This is particularly important for long-distant migrants such as lesser black-backed gulls.

Furthermore, linking individual foraging patterns to breeding success is a major next step to understand the spatiotemporal foraging behaviour of individual seabirds in greater detail (e.g. Harris et al. 2014; Jaeger et al. 2014). For instance, Lescroël et al. (2010) found that successfully breeding Adélie penguins (*Pygoscelis adeliae*) foraged more efficiently than individuals with a poor breeding success. Moreover, breeding success and chick body condition can be related to the birds' diet derived from stable isotope analyses (e.g. Kowalczyk et al. 2014). In combination with data on the individual energy expenditure which can be obtained from built-in accelerometers in the most recent data loggers, these data will help to explain the foraging habitat selection and utilization of seabirds (Halsey et al. 2008; Elliott et al. 2013). In particular, it may help to identify the energetic costs of varying flight and foraging behaviours (e.g. flapping vs. gliding; surface-feeding vs. plunge-diving). Regarding lesser black-backed gulls, their estimated energy expenditure during different foraging modes at land or sea might clarify the advantages of both foraging habitats and the underlying individual decision-making processes for habitat choice. Furthermore, accelerometer can particularly assess precise triaxial movements of individuals within offshore wind farms and therefore represent a useful tool for the above-mentioned impact assessments.

A further future aspect will be to combine the tracking data with habitat suitability modelling to assess food availability and the complex interactions with varying environmental conditions (e.g. Louzao et al. 2011; Fedak 2013). Therefore, several indirect proxies are currently used, e.g. chlorophyll-a concentration, salinity or sea surface temperature. With the help of such oceanographic features, which can be recorded by several integrated sensors in tags, habitat suitability can be obtained, and thus the effects of environmental change on seabird foraging behaviour can be assessed (e.g. Bost et al. 2008; Skov et al. 2008; Evans et al. 2013). For instance, potential associations of lesser black-backed gulls with oceanographic parameters and derived information of prey availability will help to identify and understand general changes and trends in their foraging distribution. Fedak (2013) introduced the opportunities of ocean profiling tags, primarily for diving species such as northern gannets, which might not least provide important implications for conservation and management issues.

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AUTHOR CONTRIBUTION

This thesis is based on four different manuscripts, which have already been published, are currently under revision or submitted to peer-reviewed scientific journals. In the following, I will describe my own contribution and that of all other authors to these manuscripts.

I Varying foraging patterns in response to competition? A multi-colony approach in a generalist seabird (Chapter I)

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Author contribution: AMC and SG developed the idea for the manuscript. BM conducted fieldwork between 2008 and 2011. CCV performed the stable isotope analyses. AMC conducted fieldwork between 2011 and 2013, and analysed all data. AMC wrote the manuscript. SG, BM and CCV reviewed and approved the manuscript.

II Individual factors influencing sexual segregation in foraging habitats in a marine top predator (Chapter II)

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III What flight heights tell us about foraging and potential conflicts with wind farms: a case study in lesser black-backed gulls (*Larus fuscus*) (Chapter III)

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Author contribution: AMC and SG developed the idea for the manuscript. AMC conducted fieldwork, and analysed all data. AMC wrote the manuscript. SG reviewed and approved the manuscript.

IV Marine wind farms, fisheries and northern gannets: a pilot study in the southern North Sea (Chapter IV)

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ERKLÄRUNG

Hiermit erkläre ich, dass ich die vorliegende Arbeit selbstständig angefertigt habe und dass sie in Inhalt und Form meine eigene Arbeit ist. Abgesehen von der Beratung meines wissenschaftlichen Betreuers, wurden keine anderen als die angegebenen Hilfsmittel und Quellen genutzt. Die Arbeit wurde unter Einhaltung der Regeln guter wissenschaftlicher Praxis der Deutschen Forschungsgemeinschaft erstellt.

Dies ist mein erster Promotionsversuch. Diese Arbeit wurde weder ganz noch zum Teil an einer anderen Stelle im Rahmen eines Prüfungsverfahrens vorgelegt.

Für die mündliche Prüfung wird die Form der Disputation gewählt. Der Zulassung von Zuhörerinnen und Zuhörern bei der Disputation wird nicht widersprochen.

Büsum, den 02.07.2015

Anna-Marie Corman