SEASONAL VARIATION IN TROPHIC NICHE AND RESOURCE USE IN GREAT BLACK-BACKED GULLS *LARUS MARINUS*

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ABSTRACT

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Seabirds experience variable extrinsic and intrinsic pressures throughout the annual cycle that affect their ability to forage. Consequently, their foraging strategies may vary between breeding and non-breeding seasons due to the constraints of central-place foraging during the former. Here, we studied a population of a generalist seabird, the Great Black-backed Gull *Larus marinus*, breeding at a colony on the Isle of May, Scotland. We quantified seasonal variation in sexual segregation, trophic position, trophic niche width, and resource use by examining stable isotopes in feathers collected from adults. We found no sexual segregation, but we detected population- and individual-level shifts in trophic position, trophic niche width, and resource use throughout the annual cycle, providing novel information about the ecology of the Great Black-backed Gull. The population was most specialised during the late non-breeding period, when marine resources made up over 95% of the population's diet. During breeding, terrestrial resources made up 20% of the population's diet, and a much greater percentage for some individuals. We highlight the importance of undertaking trophic studies beyond the breeding period to advance collective knowledge of species' ecology and to improve assessments of the potential impacts of environmental change and other anthropogenic threats during the non-breeding season, which is critical for seabird survival.

Key words: stable isotope analysis, foraging ecology, trophic dynamics, diet, seabird ecology

INTRODUCTION

Throughout their annual cycle, seabirds experience extrinsic and intrinsic constraints on their ability to feed, survive, and reproduce, which are imposed by the environment and their life history. Notably, there is seasonal variation in access to resources as well as in the availability and distribution of prey. These variations most typically occur between breeding and non-breeding seasons, when the central-place foraging constraint is present and absent, respectively (Jessopp et al., 2020). Such constraints are key determinants of the intra- and inter-specific competition that shape individual foraging strategies and ultimately define population-level resource use and trophic niche width (Gulka et al., 2017; Jessopp et al., 2020; Maynard et al., 2021). Populations of generalist seabirds may comprise individuals with different foraging strategies (Phillips et al., 2017). Under conditions of high prey availability or little intra-specific competition, individuals may be able to exploit the same resources, causing the population-level trophic niche width to become narrower (i.e., more specialised; Gulka et al., 2017). When prey availability is relatively predictable but no single resource is abundant enough to offset intra-specific competition, segregation between individuals may occur (Phillips et al., 2017). Such conditions can lead to populations having a wide trophic niche, where individuals are relatively specialised and exploit smaller sections of a broader niche of the total population, thus reducing intra-specific competition and improving foraging efficiency (Phillips et al., 2017). Common mechanisms of foraging segregation include sexual differences (i.e., divide between males and females; Calado et al., 2020; Phillips et al., 2011) or individual specialisation, whereby individuals develop different foraging strategies that are not attributable to any discrete or measurable variables such as sex, ontogeny, or morphology (Araújo et al., 2011; Bolnick et al., 2003; Phillips et al., 2017). Lastly, highly dynamic and unpredictable environments may drive individuals to act as generalists, with all individuals using a similarly broad range of resources (Bolnick et al., 2003; Dehnhard et al., 2020; Phillips et al., 2017). Generalist populations may therefore be complex in structure and composed of individuals with a spectrum of foraging strategies. Crucially, these strategies may vary in response to changes in extrinsic and intrinsic pressures.

The relative positions of individuals and populations on the specialisation spectrum are of conservation importance. For example, specialisation within generalist populations may result in subsets of individuals being impacted by the degradation of a single habitat or resource while the remaining specialist or generalist individuals are relatively unaffected (Phillips et al., 2017). If such degradation affects a small proportion of individuals, population-level consequences may be small, unless these subsets play an important role as buffers within populations. However, if foraging segregation leads to a large proportion of individuals (e.g., one of the sexes; Jiménez et al., 2016) being impacted by a particular threat, population-level consequences could be significant. Undertaking ecological studies at both the individual and the population levels therefore provides finer-scale information that can be used to better assess the potential consequences of changes in resource availability and anthropogenic threats on populations.

Seabirds face different external pressures and life history decisions throughout the annual cycle, and their foraging strategies are likely to vary seasonally. During the non-breeding season, adult seabirds shift their focus from reproduction to survival and feather moult. As the subsequent breeding attempt approaches, they also focus on improving their body condition. Because environmental conditions are typically harsher during the non-breeding season, particularly in temperate and polar species, the highest mortality occurs at this time (Harris & Wanless, 1996). Historically, most existing knowledge about the foraging ecology of seabirds has been limited to the breeding season because, as central-place foragers, individuals return to breeding colonies where they can be closely monitored and studied (Barrett et al., 2007; Mitchell et al., 2004). The development of biochemical diet analysis techniques, such as stable isotope analysis, and miniaturised data loggers has greatly improved our knowledge of seabird ecology during the non-breeding season (Calado et al., 2020; Nielsen et al., 2018; Yoda, 2019). Such studies have shown seabirds may use different foraging strategies during the non-breeding season, exploiting different prey and habitats (Kowalczyk et al., 2015; Meier et al., 2017; Ronconi et al., 2010). However, for many species and populations, there is still little knowledge about the resources and habitats used by individuals outside of the breeding season. These knowledge gaps may present important barriers when assessing and predicting the effects of environmental change on seabird populations. The gaps also inhibit seabird management and conservation, as policy makers have incomplete knowledge of the resources and habitats on which the birds rely during critical periods of the annual cycle. Studies that integrate year-round trophic data therefore provide a more holistic approach to understanding the ecology of species and their seasonally varying requirements.

The Great Black-backed Gull *Larus marinus* inhabits temperate and arctic coasts of the North Atlantic Ocean. It feeds on a wide variety of prey, including natural prey such as intertidal organisms, pelagic fish, mammals, and seabirds, as well as anthropogenic resources such as refuse, agricultural products, and fish discards (Coulson, 2019). The species has an almost exclusively coastal breeding distribution. In the western North Atlantic, Great Black-backed Gulls showed slight seasonal variation in trophic level, with populations typically foraging at a higher trophic level during breeding compared to non-breeding. Marine prey such as fish, crabs, clams, and seal carcasses dominates their diet year-round (Ronconi et al., 2014; Steenweg et al., 2011). Additionally, body size or sex (which are correlated in the species, males being around 20% larger than females; Mawhinney & Diamond, 1999) may also drive differences in prey choice (Ronconi et al., 2014). Less is known about the foraging ecology of Great Black-backed Gulls in the eastern North Atlantic, and no studies have examined their diet beyond the breeding season. In Europe, Great Black-backed Gulls occupy coastal habitats, where there is potentially increased availability of marine resources in the form of other seabirds and forage fish during the breeding season (Westerberg et al., 2019). Forage fish sustain a large number of diving and surface-feeding seabirds during the breeding season in the North Sea (Furness & Tasker, 2000). Furthermore, Great Black-backed Gulls also forage on terrestrial prey in agricultural and urban areas (O'Hanlon et al., 2025). Consequently, they would be expected to modify their foraging behaviour and diet in response to seasonally varying prey availability and central-place foraging constraints. The objective of this study was therefore to examine seasonal differences in the foraging ecology of Great Black-backed Gulls in the population on the Isle of May, Scotland. More specifically, we used stable isotope ratios of nitrogen ($^{15}N/^{14}N$) and carbon ($^{13}C/^{12}C$) from feathers to quantify seasonal variation in sexual segregation, trophic position, trophic niche width, and resource use during the annual cycle.

MATERIALS AND METHODS

Study System

The Isle of May National Nature Reserve in Scotland (56°11′09.5″N; 002°33′21.3″W) is located in the Firth of Forth and has a breeding population of approximately 120 pairs of Great Black-backed Gulls (2021 census; Langlois Lopez et al., 2023; Fig. 1). This locality is situated ~8 km southeast from the coast of Fife, which is dominated by rocky shores, small fishing harbours, and extensive agricultural land. The coast of Lothian, also dominated by rocky shores and extensive agricultural land, is situated ~15 km to the southwest. The island also has internationally important populations of other seabirds, including 52,000 pairs of Atlantic Puffin *Fratercula arctica*; 15,000 pairs of Common Guillemots *Uria aalge*; 3,800 pairs of Razorbills *Alca torda*; 2,500 Black-legged Kittiwakes *Rissa tridactyla* (NatureScot, 2024), and a population of European Rabbits *Oryctolagus cuniculus*, all known to be prey species of Great Black-backed Gulls (Bennett, 2017; Langlois Lopez et al., 2023).

On the Isle of May, Great Black-backed Gulls typically commence egg laying in the second or third week of April with a peak in early May, and chicks reach fledging size by the middle of July (Langlois Lopez et al., 2024). After breeding, Great Black-backed

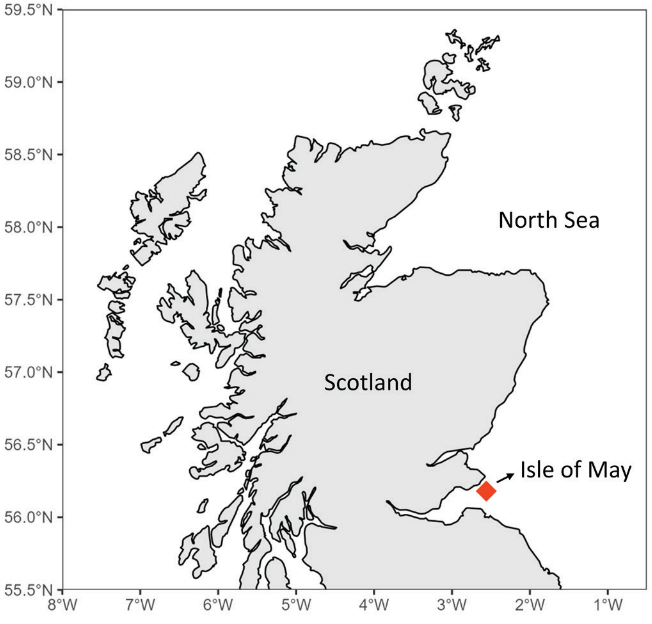


Fig. 1. Location of the study site of the Isle of May (orange diamond) in Scotland.

Gulls from the Isle of May and rest of the United Kingdom (UK) are known to predominantly remain in the UK during the non-breeding period, primarily along North Sea coasts and in the vicinity of their breeding colonies (Wernham, 2002). This lack of migration contrasts with more northerly populations from Fennoscandia and Russia that undertake longer non-breeding movements (Wernham, 2002). Therefore, Great Black-backed Gulls from our study site have access to natural and anthropogenic resources of terrestrial and marine origin throughout their annual cycle, but they are constrained in their use by extrinsic and intrinsic pressures such as central-place foraging and prey availability.

Stable Isotope Analysis

In ecological studies, analysis of the ratios of stable isotopes of nitrogen ($^{15}N/^{14}N$) and carbon ($^{13}C/^{12}C$) offers a robust technique to investigate the diet and trophic niche characteristics of individuals and populations across different spatiotemporal scales (Crawford et al., 2008; Inger & Bearhop, 2008). In marine environments, the ratio of the heavier and rarer ^{15}N to the more common ^{14}N increases in a predictable manner as it ascends through the trophic chain, typically at a rate of 3‰–5‰ per trophic level, facilitating the identification of the trophic level in which a consumer feeds. The $^{13}C/^{12}C$ ratio remains relatively stable between trophic levels, but it can be used to infer the carbon source of consumers because organisms from marine environments typically have higher carbon ratios than terrestrial organisms, particularly those from benthic and intertidal environments (Hobson et al., 1994). The combined use of carbon and nitrogen isotopic data can be used to quantify trophic niche width (Newsome et al., 2007). Furthermore, the development of stable isotope mixing models using a Bayesian approach has increased the ability to make inferences from stable isotope data, including the improved estimation of trophic niche width, the estimation of resource contribution to the diet of an individual or population, and robust statistical comparisons between or within populations (Jackson et al., 2011; Stock et al., 2018).

Here, we analysed carbon and nitrogen stable isotope ratios from feather samples. Feathers become metabolically inert after being grown, meaning that their nitrogen and carbon isotopic values reflect dietary information from when the tissue was grown, over a period of weeks (Inger & Bearhop, 2008). All stable isotope values are reported in the delta "δ" notation, where $\delta^{13}C$ or $\delta^{15}N$ = [(Rsample/Rstandard) – 1]1000, and where R is the ratio $^{13}C/^{12}C$ or $^{15}N/^{14}N$. The global standard for $\delta^{13}C$ is Pee Dee Belemnite, and the standard for $\delta^{15}N$ is atmospheric nitrogen.

Bird Capture and Feather Sampling

The moult strategy of Great Black-backed Gulls is well understood, with different feather groups moulted in consistent patterns: primary feathers commence moulting during the early breeding season (incubation), secondary feathers during the autumn and early winter, and contour feathers around the nape and face during late winter (Demongin, 2016; Ingolfsson, 1970). Thus, strategic sampling of these feather types can provide the isotopic signature of an individual throughout the annual cycle.

Between 01 May and 20 June 2021, 35 breeding adult Great Black-backed Gulls were captured at the nest using walk-in traps (three birds), spring traps (one bird), and a leg noose (31 birds) to obtain feather samples. Where possible, nests with known laying dates were targeted, and trapping was undertaken during the second half of incubation to allow birds to establish a strong bond with their nests prior to trapping and to limit the risk of abandonment due to handling. Additionally, only one individual was targeted per nest to avoid potential negative handling impacts affecting both members of a pair. From each bird, biometric measurements (to the nearest mm) and mass (to the nearest gram) were taken for sexing purposes, following the methods of Mawhinney & Diamond (1999; n = 18 females and n = 17 males). Biometric measurements included head and bill, bill length to feather, bill depth at gonys, minimum tarsus, and wing length. All birds were fitted with a metal British Trust for Ornithology (BTO) ring and an individually marked alpha-numeric colour-ring. Approximately ten white barbs were clipped from the tip of the inner primary P1 (the first primary to be moulted), middle secondary S8 (the last secondary to be moulted), and nape feathers (Fig. 2). We avoided black barbs because high amounts of melanin may alter isotopic values (Michalik et al., 2010). Feather samples were kept dry in paper envelopes until sample preparation and analysis. During the sampling of primary feathers, some birds had already shed P1, in which case we sampled the next available primary following the moulting order. We assumed this did not affect our results, since some individual variation in the timing of moult is expected, and all primary feather samples obtained, regardless of whether they came from P1, P2, or P3, would have been moulted during the 2020 breeding season. Overall, we obtained feather samples that represented the following seasons: May–June 2020 (primaries), October–December 2020 (secondaries), and January–February 2021 (nape). In phenological terms, we assigned these to breeding (incubation), early non-breeding, and late non-breeding, respectively.

Diet Sampling

In preparation for the use of stable isotope mixing models to quantify the diet of Great Black-backed Gulls, we opportunistically collected prey items for stable isotope analysis that were either found within the colony or regurgitated by adults or their chicks during sampling and ringing procedures. We sampled muscle tissue from fish, mammals, crustaceans, and cephalopods that were known to be eaten by Great Black-backed Gulls from observations and examination of carcasses. The use of muscle is recommended over whole-body samples to minimise variation in isotopic values (Becker et al., 2007). All samples collected were kept frozen in sealed zip-lock bags until sample preparation and analysis.

A potential limitation of longitudinal isotopic studies in seabirds is that resource use during non-breeding and breeding seasons may not be isotopically comparable if individuals move or migrate between regions with significantly different isoscapes, i.e., different baseline

Fig. 2. Diagram of a Great Black-backed Gull *Larus marinus* showing the three feather types sampled in the study (primary P1, secondary S8, and nape) and their respective moult seasons.

δ^{13}C and δ^{15}N values of primary producers, which are determined by the biochemical and physical properties of local carbon and nitrogen sources (St John Glew et al., 2021). Although regional differences in baseline isotopic values between breeding and wintering areas are possible in our study system, it would be unlikely for these to be large enough to significantly change the findings of our mixing models, since we quantified resource use at a coarse scale (see below). Therefore, we assumed that despite collecting prey items only during the breeding period, their isotopic characteristics would be representative of the type of resources gulls access year-round.

Due to the broad diet of Great Black-backed Gulls, we were unable to obtain samples from all potential prey sources at our study site. Thus, we obtained δ^{13}C and δ^{15}N values from additional prey items (demersal fish, grain, terrestrial invertebrates, and refuse) that are known to be present in the diet of Great Black-backed Gulls and other generalist gulls from published literature. A default standard deviation of 1 was used for prey items with a sample size of one (i.e., grain).

Sample Preparation

Feather samples were washed and rinsed in two separate solutions: a diluted detergent solution (1:50 Ecover laundry detergent to deionised water) and a 0.25 M sodium hydroxide solution, both of which have been previously used to eliminate impurities and oils that might be present on feathers (Bearhop et al., 2002; Paritte & Kelly, 2009). Using tweezers, feather samples were first washed in the detergent solution for 30 seconds, then consecutively rinsed in three beakers of distilled water and air dried. The same protocol was then followed using the sodium hydroxide solution.

Prey samples that likely were enriched with lipids (i.e., muscle tissue of fish, seabirds, cephalopods, and crustaceans), and thus depleted in ^{13}C, were subjected to a lipid-extraction process following Elliott et al. (2017). However, because lipid extraction can impact δ^{15}N values (Bodin et al., 2007; Sweeting et al., 2006), each sample was split in two and only one half was extracted, from which the δ^{13}C values were obtained. We then obtained δ^{15}N values from the non-extracted half. Samples were first oven-dried at 50 °C for 48 hours. Once dried, they were ground to small fragments or a powder. The samples intended for lipid extraction were subjected to three rinses in a 2:1 chloroform-methanol solution. Each sample was placed in an individual glass vial containing the solution. The vial was agitated on a shaker at room temperature for 15 minutes, then centrifuged for three minutes to separate the lipids and solution from the tissue. This protocol was repeated three times per sample. After the rinse procedure, we confirmed that the carbon to nitrogen ratios of lipid-extracted samples were less than 3.5, which is the threshold below which δ^{13}C values are considered reliable and not negatively biased due to ^{13}C depletion (Post et al., 2007).

Sample Analysis

For the stable isotope analysis, aliquots of 0.7 mg per sample were placed in tin capsules, which were combusted and analysed using an elemental analyser system (Elementar Pyrocube) connected to a Delta XP isotope ratio mass spectrometer (Thermo Fisher Scientific) at the National Environmental Isotope Facility (NEIF) Stable Isotope laboratory in East Kilbride, Scotland. Three lab standards (Sigma Aldrich) were analysed after every 10 unknown samples: Gelatine (Fluka gelatine), Alagel (a mixture of gelatine and alanine), and Glygel (a mixture of gelatine and glycine). The Gelatine lab standard was used to correct instrument linearity, and replication of the three lab standards was used to correct for instrument drift over a 22-hour analytical run. Four replicates of USGS40 (glutamic acid; Sigma Aldrich) were analysed as unknowns with each analytical run, and their standard deviations were 0.01‰ for δ^{13}C and 0.17‰ for δ^{15}N ($n = 12$).

Data Analysis

All statistical analyses were performed using various packages in the software program R, version 4.0.4 (R Core Team, 2021).

Sexual segregation and seasonal variation in trophic niche

To investigate whether there was sexual segregation and seasonal variation in the trophic position (i.e., δ^{13}C and δ^{15}N values) of the population throughout the annual cycle, we built separate Linear Mixed Models (LMMs) using the “lme4” R package (Bates et al., 2015) for the response variables δ^{13}C and δ^{15}N. LMMs included sex (male and female) and season (breeding, early non-breeding, late non-breeding) as fixed effects, and bird ID as a random effect to account for repeated measures from each individual (three feather types representing three different seasons per bird). We also considered an interaction term between sex and season to test whether sexual segregation varied between seasons. We used Akaike Information Criterion (AIC; Akaike, 1973) for model comparison using a threshold of two units to identify the best supported models (Zuur et al., 2009). Models were validated by visually inspecting standardised residuals to confirm homogeneity of variance and normality. Once the best supported models were identified, we carried out post-hoc analyses using estimated marginal means and p values adjusted using Tukey’s method (using the “emmeans” R package; Lenth et al., 2018) to estimate differences between seasons and sexes.

To investigate whether there was seasonal variation in the population’s trophic niche width, as well as sex differences, we used the “SIBER” R package (Jackson et al., 2011) in combination with the “rjags” R package (Plummer, 2018) to estimate and statistically compare standard ellipse areas using a Bayesian framework (SEAb) as well as standard ellipse areas corrected for small sample sizes (SEAc). Standard ellipse areas provide a measure of trophic niche width that contains approximately 40% of the isotopic data, combining δ^{13}C and δ^{15}N values to quantify trophic niche width in a two-dimensional isotopic space. We compared SEAb between sexes across all seasons, and we compared between seasons with sexes pooled to assess shifts in trophic niche width at the population level. These pairwise comparisons were carried out by calculating the proportion of simulations in which the SEAb of a season or sex (e.g., breeding) was larger than the other (e.g., late non-breeding) using a significance level of 5% (Jackson et al., 2011). We ran 10,000 Markov-chain Monte Carlo simulations to generate SEAb and their 95% credible intervals. SEAc were produced using maximum likelihood for additional comparisons (without confidence intervals) and visualisation purposes. Additionally, the mean niche overlap was also calculated from the posterior distributions of SEAb to assess trophic niche similarity between sexes and seasons.

Seasonal variation in resource use

To estimate the contribution of different food items to the diet of Great Black-backed Gulls and to quantify their seasonal variation, we used stable isotope mixing models run with the "MixSIAR" R package (Stock et al., 2018) and the "rjags" R package (Plummer, 2018). These packages also use a Bayesian framework and are able to account for uncertainty in the isotopic values of prey items and trophic enrichment factors (TEFs; the shift in isotopic values of a consumer compared to those of the food it is eating). Due to the large number of prey sources with similar isotopic signatures, which introduces uncertainty in mixing models, we used both a priori and a posteriori prey groupings to better quantify the contribution of marine and terrestrial resources to the diet of Great Black-backed Gulls, at the expense of prey taxonomic resolution (Phillips et al., 2005). The a priori grouping was undertaken before running model validations and stable isotope mixing models by grouping prey items with similar isotopic values from similar trophic levels and habitats into a single trophic group. This step reduced our prey sources from 15 to seven (Table 1). However, high uncertainty around the contribution of each marine source was still present due to their similar isotopic values (Fig. A1). Consequently, we grouped all a posteriori marine resources into a single category (Table 1).

To estimate resource use at the population level, MixSIAR stable isotope mixing models were run with sexes pooled and season (i.e., breeding, early non-breeding, late non-breeding) as a fixed effect. Additionally, to estimate resource use at the individual level, separate MixSIAR stable isotope mixing models were run for each season, with individual ID as a fixed effect. We ran 1,000,000 iterations per model, with a burn-in period of 500,000 and a thinning rate of 500. Lastly, model outputs were validated by confirming model convergence using the Geweke and Gelman-Rubin diagnostic tests (Stock et al., 2018).

Appropriate TEFs are essential to obtain robust results from stable isotope mixing models. However, empirically calculated TEFs are lacking for most wild animals because obtaining them requires absolute control over an animal's diet and periodic sampling of the animal's tissues, which realistically can only be achieved with captive individuals (see Hobson & Clark, 1992). Empirical estimates of TEFs for some bird species are available, and these are generally used to inform studies of species lacking such data (see Calado et al., 2020; Lato et al., 2021). However, TEFs of feathers vary considerably across seabird species (Becker et al., 2007). Thus, we considered three sets of TEFs, two from gulls species of the same genus as Great Black-backed Gulls (Ring-billed Gull *Larus delawarensis* (3.0‰ ± 0.2‰ for nitrogen, 0.2‰ ± 1.3‰ for carbon; Hobson & Clark, 1992) and Black-tailed Gull *Larus crassirostris* (5.3‰ ± 0.8‰ for nitrogen, 3.6‰ ± 0.5‰ for carbon; Mizutani et al., 1992), as well as a mean value across multiple seabird species (3.6‰ ± 1.0‰ for nitrogen, 1.4‰ ± 1.0‰ for carbon; Becker et al., 2007).

To validate prey isotopic data as well as TEFs for their use in stable isotope mixing models, we used a method described by Smith et al. (2013), which uses mixing polygons to infer whether a consumer's diet is represented by the prey sources and TEFs used. If all consumer isotopic data fall within the mixing polygon, the diversity of prey sources is considered to appropriately represent the consumers' diet, and it can be assumed that no important prey source has been missed. We ran three validation models of 1,500 iterations, with the three sets of TEFs, using the a priori prey groups, and the consumers' isotopic data across all seasons (*n* = 104).

RESULTS

Sexual Segregation and Seasonal Variation in Trophic Position

The models to explain differences in $\delta^{13}C$ and $\delta^{15}N$ values across seasons were equally supported whether they contained season and sex, or only season, as explanatory variables (Table A1). Therefore, sex did not have a statistically significant effect on $\delta^{13}C$ and $\delta^{15}N$

TABLE 1
Summary of a priori and a posteriori grouping of prey items to inform stable isotope mixing models for Great Black-backed Gull *Larus marinus* on the Isle of May, Scotland

Prey sources	A priori grouping	A posteriori grouping
Grain	Anthropogenic terrestrial (Urban/agricultural)	Anthropogenic terrestrial (Urban/agricultural)
Unidentified invertebrate		
Refuse		
European Rabbit *Oryctolagus cuniculus*	Natural terrestrial	Natural terrestrial
Fish Clupeidae spp.	Forage fish	Marine
Fish Gadidae spp.		
Fish Ammodytidae spp.		
Large unidentified fish	Large unidentified fish	
Whiting *Merlangius merlangus*	Demersal fish	
Plaice *Pleuronectes platessa*		
Haddock *Melanogrammus aeglefinus*		
Velvet Swimming Crab *Necora puber*	Intertidal	
Unidentified cephalopod		
Common Eider duckling *Somateria mollissima*	Seabirds	
Atlantic Puffin *Fratercula arctica*		

values ($F_{1,33} = 0.021$, $P = .885$; $F_{1,33} = 1.074$, $P = .231$, respectively), although males had slightly higher δ^{15}N values than females (Table 2). However, both δ^{13}C and δ^{15}N values differed significantly across seasons ($F_{2,67} = 15.097$, $P < .001$; $F_{2,67} = 20.82$, $P < .001$, respectively).

To better portray differences between seasons at the population level, we carried out pairwise comparisons with sexes pooled because there were no significant differences between sexes in δ^{13}C or δ^{15}N values (Fig. 3). We found that δ^{15}N values during late non-breeding were significantly higher than during breeding and early non-breeding, but we noted no significant differences between breeding and early non-breeding. This showed that Great Black-backed Gulls foraged at a higher trophic level during late non-breeding (i.e., January–February of 2021;

TABLE 2

Summary of feather types sampled from male and female Great Black-backed Gulls *Larus marinus* on the Isle of May, Scotland, including the season when they were moulted and their δ^{13}C and δ^{15}N isotope values (mean ± standard deviation)

Feather type	Moult season	Sex	*N*	δ^{13}C (‰)	δ^{15}N (‰)
Primary (P1–P3)	May–June 2020 (Breeding; incubation)	Male	17	−18.2 ± 2.5	16.7 ± 1.6
		Female	18	−18.9 ± 2.4	15.8 ± 2.6
Secondary (S8)	October–December 2020 (Early non-breeding)	Male	16	−17.5 ± 1.8	16.2 ± 2.1
		Female	18	−17.3 ± 2.3	15.9 ± 2.6
Nape	January–February 2021 (Late non-breeding)	Male	17	−16.3 ± 1.4	18.6 ± 1.3
		Female	18	−16.2 ± 1.5	18.0 ± 1.2

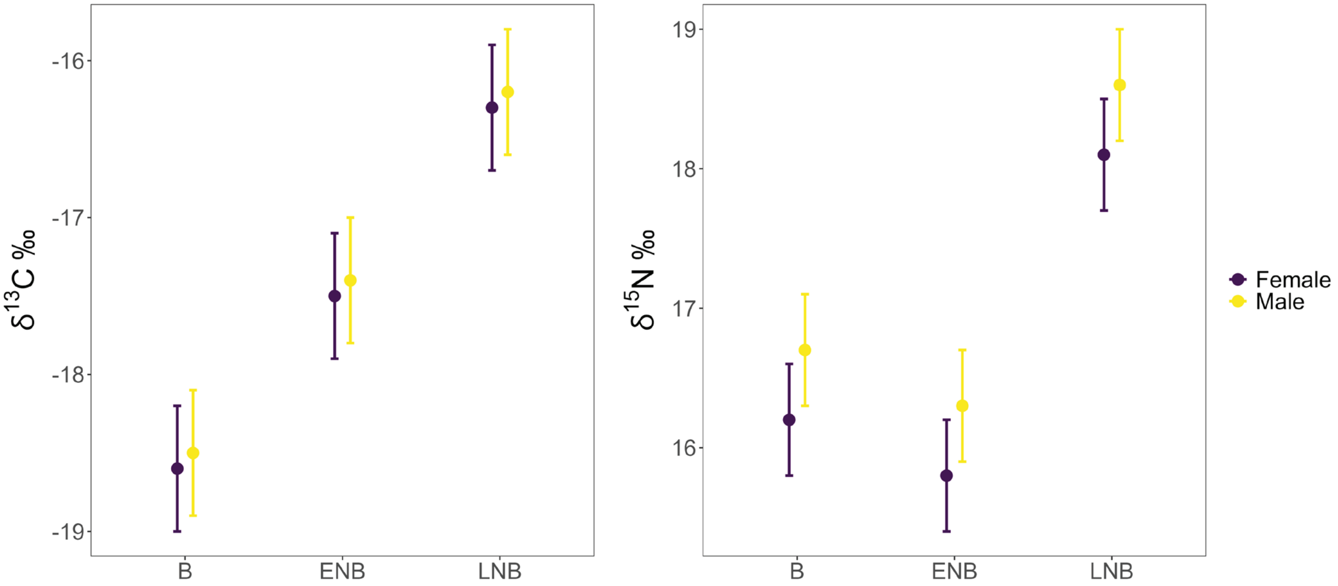


Fig. 3. Estimated marginal means and standard errors of δ^{13}C and δ^{15}N values determined from Great Black-backed Gull *Larus marinus* feathers during breeding (B), early non-breeding (ENB), and late non-breeding (LNB) periods, separated by sex.

TABLE 3

Pairwise comparisons of δ^{15}N and δ^{13}C values between seasons determined from Great Black-backed Gull *Larus marinus* feathers collected on the Isle of May, Scotland, between May 2020 and February 2021[a]

Pairwise comparisons	Isotope	Estimate	SE	*DF*	*t*	*P*	Effect direction
B I ENB	δ^{15}N	0.40	0.37	67.00	1.07	.791	-
	δ^{13}C	−1.11	0.42	67.00	−2.67	**.016**	B < ENB
B I LNB	δ^{15}N	−1.84	0.36	67.00	−4.99	**< .001**	B < LNB
	δ^{13}C	−2.26	0.41	67.00	−5.50	**< .001**	B < LNB
ENB I LNB	δ^{15}N	−2.24	0.47	67.00	−6.02	**< .001**	ENB < LNB
	δ^{13}C	−1.15	0.42	67.00	−2.78	**.016**	ENB < LNB

[a] Significant differences are highlighted in bold. B = breeding, ENB = Early non-breeding, LNB = Late non-breeding, SE = standard error, DF = degrees of freedom

Table 3, Fig. 3). Similarly, there were significant differences in δ^{13}C values between all seasons: late non-breeding had the highest values, followed by early non-breeding and breeding, showing that Great Black-backed Gulls shifted to more carbon-enriched prey during early non-breeding and late non-breeding seasons (Table 3, Fig. 3). Overall, the shifts in δ^{13}C and δ^{15}N values detected between seasons were mirrored between sexes (Fig. 3), suggesting both sexes responded similarly to changes in extrinsic and intrinsic constraints throughout the annual cycle.

Sexual Segregation and Seasonal Variation in Trophic Niche Width

There were no significant differences in trophic niche width, measured as SEAb, between males and females during any season (Table 4). A mean SEAb overlap of between 25% and 32%, suggested that sexes had similarly sized trophic niche widths and that the prey diversity consumed was also similar (Fig. 4). This agrees with the results from the LMMs in that there was no clear sexual segregation in either trophic position or niche width in the population.

TABLE 4

Summary of Bayesian Standard Ellipse Areas (SEAb) and Standard Ellipse Areas corrected for small sample size (SEAc) calculated as mean (confidence interval) for male and female Great Black-backed Gulls *Larus marinus* on the Isle of May, Scotland, during the breeding, early non-breeding, and late non-breeding seasons in 2020/21

Season	SEAc		SEAb			
	Male	Female	Male (CI)	Female (CI)	*P*	Overlap (%)
Breeding	10.2	15.8	10.2 (5.9–16.0)	15.2 (9.0–23.7)	.116	31.9
Early non-breeding	7.5	7.8	7.4 (4.2–11.8)	7.7 (4.5–12.0)	.445	32.2
Late non-breeding	5.5	3.7	5.3 (3.1–8.4)	3.7 (2.2–5.8)	.145	25.2

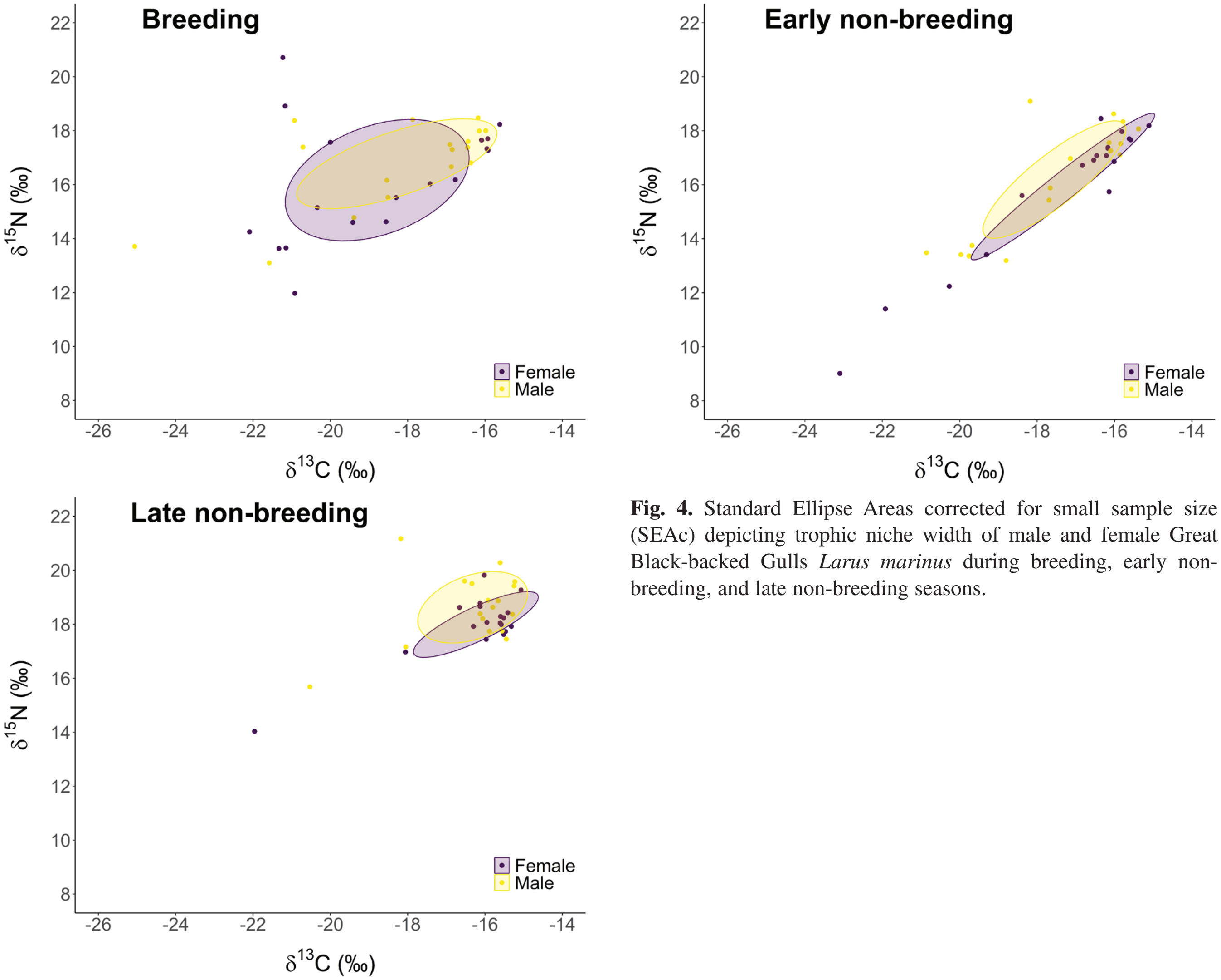


Fig. 4. Standard Ellipse Areas corrected for small sample size (SEAc) depicting trophic niche width of male and female Great Black-backed Gulls *Larus marinus* during breeding, early non-breeding, and late non-breeding seasons.

Trophic niche width was not significantly different between sexes in any season. Therefore, we pooled these data to carry out population-level comparisons. At the population level, there were significant differences in trophic niche width between breeding and early non-breeding, and between breeding and late non-breeding, but not between early non-breeding and late non-breeding (although the latter comparison was only marginally not significant; Table 5). This suggested that Great Black-backed Gulls had a more diverse diet at the population level during breeding, indicated by the larger SEAb and SEAc (Table 5, Fig. 5). During early non-breeding, and particularly during late non-breeding, the population's trophic niche width reduced almost three-fold, indicating the population was much more specialised in late non-breeding. Additionally, niche overlap between breeding and late non-breeding was minimal (~10%; Table 5, Fig. 5), suggesting not only a reduction in trophic niche width but also a population-level shift in prey choice during late non-breeding. This agreed with the results from previous LMMs, which showed a significant increase in trophic level (i.e. higher δ^{15}N values).

Seasonal Variation in Resource Use

Validation of prey sources and trophic enrichment factors

Stable isotope analysis of food samples yielded a large range of δ^{13}C and δ^{15}N values. Food items from terrestrial environments and lower trophic levels had the lowest values, and food items from marine environments, particularly those of demersal and intertidal origin, had the highest (Table 6).

Model validation with TEFs from Ring-billed Gulls and Black-tailed Gulls resulted in some of the Great Black-backed Gull isotopic data falling outside of the mixing polygons (Fig. 6). However, the TEFs reported by Becker et al. (2007) yielded a good fit with all data points within the 95% outline of the mixing polygon (Fig. 6). These latter values were therefore selected to run stable isotope mixing models.

Resource use

Marine prey contributed the most to Great Black-backed Gull diet at the population level in all seasons, but particularly during late non-breeding, when it accounted for over 95% of the population's diet. During breeding and early non-breeding, Great Black-backed Gulls also exploited anthropogenic terrestrial resources to some extent (~19% of diet) and there was uncertainty around the contribution of natural terrestrial resources (i.e., European Rabbit), with all interquartile ranges overlapping with zero (Fig. 7).

These results agreed with the trophic niche width comparisons and LMMs results, showing that the population was more specialised during late non-breeding, when there was a shift to a higher trophic level and a reduction in the use of terrestrial resources of lower δ^{15}N and δ^{13}C values. When terrestrial resources were present in the population's diet to a greater extent, larger trophic niche widths were estimated, showing less specialisation at a population level.

Comparisons in the use of marine resources between breeding and late non-breeding (the two seasons with the greatest contrast in trophic niche width) at the individual level showed clear individual differences in the use of marine resources. While almost all individuals fed primarily on marine resources during late non-breeding, some individuals greatly increased their use of non-marine (i.e., natural or anthropogenic terrestrial) resources during breeding (Fig. 8).

DISCUSSION

In this study, we quantified seasonal variation in the foraging ecology of a population of Great Black-backed Gulls. We found no evidence of sexual segregation within the population, but there were significant differences in trophic position, trophic niche width, and resource use across three different seasons (breeding,

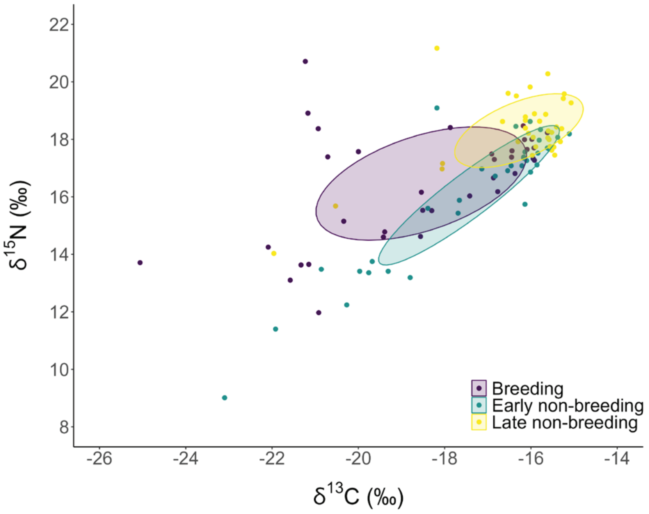


Fig. 5. Standard Ellipse Areas corrected for small sample size (SEAc) of Great Black-backed Gulls *Larus marinus* during breeding, early non-breeding, and late non-breeding seasons, with sexes pooled.

TABLE 5
Summary of Bayesian Standard Ellipse Areas (SEAb) and Standard Ellipse Areas corrected for small sample size (SEAc) of Great Black-backed Gulls *Larus marinus* on the Isle of May, Scotland, during the breeding, early non-breeding, and late non-breeding seasons in 2020/21 at the population level[a]

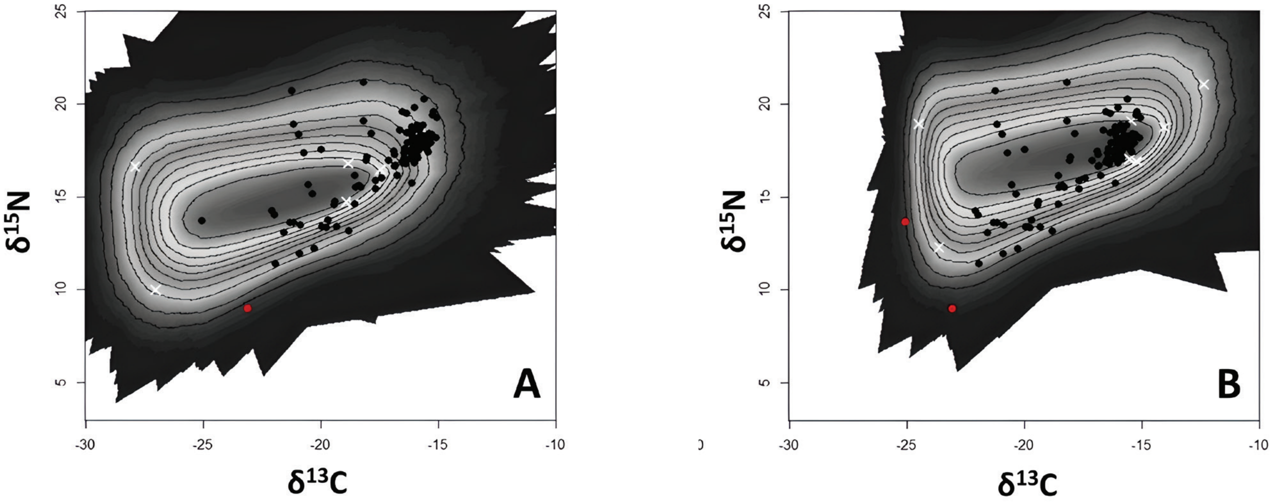
Season	SEAc	SEAb (CI)	Comparisons	*P*	Effect	Overlap (%)
B	**13.1**	**12.9 (8.9–17.6)**	**B ∣ ENB**	**.006**	**B > ENB**	**20.5**
ENB	**7.0**	**6.9 (4.8–9.5)**	**B ∣ LNB**	**< .001**	**B > LNB**	**9.6**
LNB	4.9	4.8 (3.4–6.6)	LNB ∣ ENB	.063	-	11.5

[a] Significant differences in SEAb are highlighted in bold. B = breeding, ENB = Early non-breeding, LNB = Late non-breeding, CI = confidence interval

TABLE 6
Prey items present in the diet of Great Black-backed Gulls *Larus marinus* breeding on the Isle of May, Scotland, in 2020/21 and the respective δ^{13}C and δ^{15}N isotopic values[a]

Prey sources	δ^{13}C	SD	δ^{15}N	SD	*N*	C:N	Reference
Grain	9.38	1.00	−28.62	1.00	1	-	O'Hanlon et al., 2017
Unidentified invertebrate	7.08	1.81	−27.73	0.34	5	-	O'Hanlon et al., 2017
Refuse	5.13	3.66	−23.93	2.52	2	-	O'Hanlon et al., 2017
European Rabbit *Oryctolagus cuniculus*	13.65	2.01	−28.09	0.38	5	3.17	This study
Fish Clupeidae spp.	11.09	0.42	−18.75	0.37	4	3.15	This study
Fish Gadidae spp.	11.91	0.09	−18.30	0.32	2	3.19	This study
Fish Ammodytidae spp.	11.88	0.53	−19.41	0.69	15	3.16	This study
Large unidentified fish	13.80	1.31	−19.04	1.75	5	3.35	This study
Whiting *Merlangius merlangus*	18.40	0.30	−14.60	0.60	6	-	Käkelä et al., 2007
Plaice *Pleuronectes platessa*	16.70	0.70	−14.80	0.70	6	-	Käkelä et al., 2007
Haddock *Melanogrammus aeglefinus*	12.20	0.70	−18.50	0.90	6	-	Käkelä et al., 2007
Velvet Swimming Crab *Necora puber*	13.51	0.21	−17.91	0.21	2	3.16	This study
Unidentified cephalopod	13.40	0.39	−17.41	0.55	2	3.31	This study
Common Eider duckling *Somateria mollissima*	12.74	0.06	−18.60	0.23	2	3.18	This study
Atlantic Puffin *Fratercula arctica*	10.73	0.75	−19.63	0.91	7	3.45	This study

[a] δ^{13}C and δ^{15}N are given as mean values. SD = standard deviation. C:N reflects the mean carbon to nitrogen weight ratio across sample type.



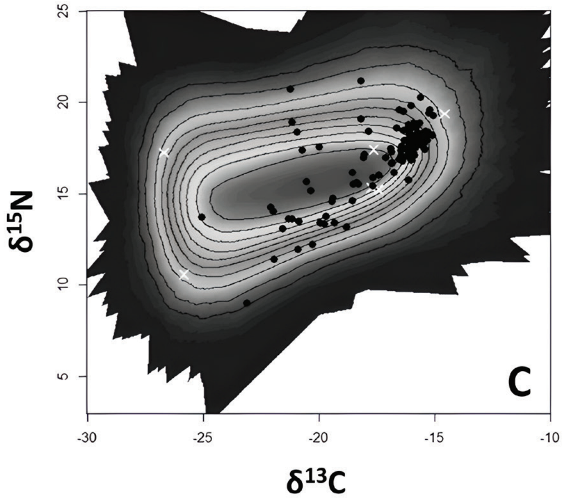


Fig. 6. Output from mixing polygon simulations to validate prey sources and trophic enrichment factors (TEFs) against Great Black-backed Gull *Larus marinus* isotopic data (black dots). Panels depict where each data point sits in relation to prey sources (white crosses). Panels A and B used TEFs from Ring-billed Gulls *Larus delawarensis* and Black-tailed Gulls *Larus crassirostris*, respectively. Panel C used a mean seabird TEF calculated by Becker et al. (2007), which is the best-fitting TEF since all data points are within the 95% contour line (i.e., the outermost solid black line). Red points indicate data points that fall outside the 95% contour lines.

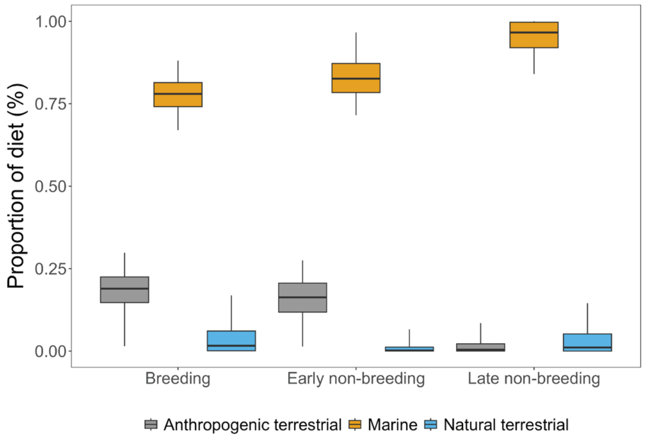


Fig. 7. Results of MixSIAR stable isotope mixing models showing the estimated contribution of different prey sources to the diet of Great Black-backed Gulls *Larus marinus* during the breeding, early non-breeding, and late non-breeding seasons. Black lines represent the median, boxes represent 50% credible intervals, and whiskers represent 95% credible intervals.

early non-breeding, late non-breeding) at the population level. Trophic position was higher and trophic niche was narrower during late non-breeding, showing that the population was significantly more specialised and fed at a higher trophic level during this season compared to the breeding and early non-breeding seasons. Such a shift to higher trophic levels corresponded with a reduction in the consumption of terrestrial resources, with over 95% of the population's diet being made up of marine resources during late non-breeding. Our findings demonstrate that the foraging ecology of Great Black-backed Gulls can vary markedly between seasons, highlighting the need for comprehensive year-round trophic studies to improve our knowledge of species' ecology and better understand how changes in resource availability may affect populations year-round.

Generalist populations may exhibit foraging segregation in response to extrinsic and intrinsic pressures to improve foraging efficiency and ultimately increase individual and population fitness (Araújo et al., 2011; Phillips et al., 2017). Sexual segregation is one such mechanism, and it is often prevalent in sexually dimorphic seabirds, including *Larus* gulls (Mancini et al., 2013). Differences in the foraging behaviour and consequently diet between males and females have been recorded in Lesser Black-backed Gulls (Enners et al., 2018). Yellow-legged Gulls *Larus michahellis* from different colonies, for example, showed year-round segregation in trophic level and niche width, with males foraging primarily on fish and females foraging on marine invertebrates and a wider prey base (Calado et al., 2020). Conversely, a lack of sexual segregation in diet and foraging behaviour has also been reported in species such as Black-tailed Gulls and Kelp Gulls *Larus dominicanus* (Kasinsky et al., 2021; Kazama et al., 2018). As generalist species, within-sex or individual variation in the diet of gulls is often greater than between sexes or populations. In our study we found no obvious sexual segregation in trophic position or niche width at any time of the year, although male feathers were on average 0.1‰–0.7‰ and 0.3‰–0.9‰ more enriched in δ^{13}C and δ^{15}N, respectively, than female feathers. This difference was not statistically significant, but suggested there were perhaps slight differences in diet, with males possibly foraging on some food items of higher trophic levels from marine environments that were not available to females, which could have been due to intra-specific competition as previously observed in other populations (Greig et al., 1985).

The lack of sexual segregation was somewhat unexpected, given the species' sexual dimorphism and previously observed differences detected between individuals with larger and smaller head sizes (which is correlated with sex) in other populations of Great Black-

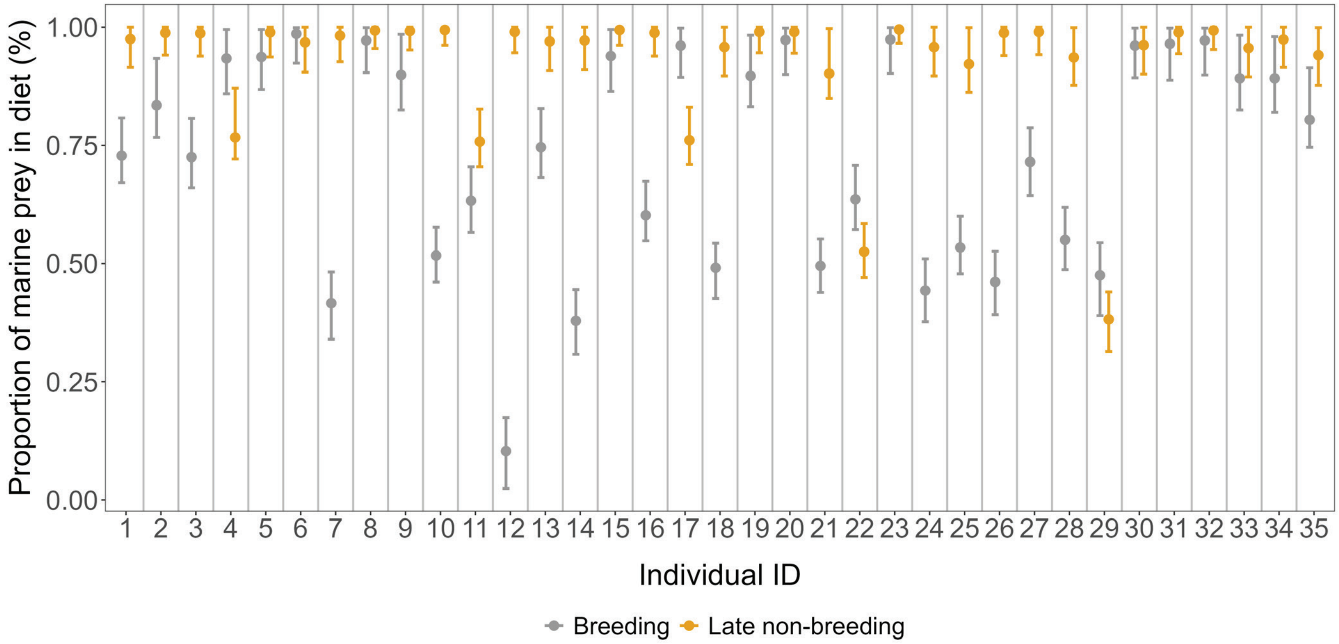


Fig. 8. Results from MixSIAR stable isotope mixing models showing the estimated contribution of marine prey to the diet of 35 Great Black-backed Gulls *Larus marinus* (identification numbers along the x axis) during the breeding (grey) and late non-breeding (orange) seasons. Points represent the median value, and bars represent 95% credible intervals.

backed Gulls (Ronconi et al., 2014). Since sexual segregation may be magnified under periods of lower food availability (i.e., higher intra-specific competition), a lack of segregation could be indicative that abundant resources were available year-round to the Isle of May population. However, it is also possible that subtle segregation occurred but was not detectable with stable isotope analysis, since many prey items consumed by Great Black-backed Gulls have overlapping isotopic signatures. Such lack of taxonomic detail also limited our ability to identify which specific resources were important for Great Black-backed Gulls beyond the coarse marine/terrestrial categories. While we identified marine resources as highly important, we could not distinguish between natural and anthropogenic marine prey (e.g., fisheries discards), which limited our ability to resolve fine-scale dietary differences. Complementary techniques such as fatty acid analysis, DNA metabarcoding, or pellet analysis (McInnes et al., 2017; Owen et al., 2013; Williams & Buck, 2010) could provide the additional taxonomic resolution needed to better assess potential sex-based differences in resource use.

Optimal foraging theory predicts foragers maximise fitness by feeding on resources that provide the highest energy gain for the lowest search time and handling cost (Stephens & Krebs, 1986). The trophic niche width of generalist predators with high foraging plasticity is thus expected to widen (generalise) or narrow (specialise) according to the availability of the most profitable prey (Gulka et al., 2017; Kowalczyk et al., 2015; Stephens & Krebs, 1986). When profitable prey is abundant, generalist consumers benefit from specialising on such prey (Davoren et al., 2012; Gulka et al., 2017; Stenhouse & Montevecchi, 1999). Our results demonstrated significant shifts in trophic position and trophic niche width during one annual cycle in Great Black-backed Gulls, suggesting that prey availability varied throughout the year. The population was least specialised (i.e., had the largest trophic niche width) during the breeding season, using terrestrial resources to a greater extent than during late non-breeding. Such a pattern was potentially driven by the constraints of central-place foraging, perhaps driving individuals to segregate in resource use. This is also suggested by the greater divide observed in the use of terrestrial and marine resources among individuals. Greater competition could have forced some individuals to feed on anthropogenic terrestrial resources, which are generally considered of lower quality (Hebert et al., 2008). Alternatively, the cost of obtaining these resources may also be lower, encouraging segregation and more efficient foraging (Borrmann et al., 2019; Jiménez et al., 2016). The greatest specialisation (i.e., the smallest trophic niche width) occurred during late non-breeding, which also corresponded with an increase in trophic level, suggesting Great Black-backed Gulls were feeding on marine prey of higher quality. Such a shift could be due to the release of Great Black-backed Gulls from central-place foraging, which could have given them the mobility required to target localised winter hotspots. Interestingly, the directionality of the seasonal shifts in trophic level in our study contrast against those recorded in Great Black-backed Gulls in the Northwest Atlantic, where the species fed at lower trophic levels during non-breeding (Ronconi et al., 2014; Steenweg et al., 2011). This difference may be due to Great Black-backed Gulls using primarily marine resources year-round at study sites in the Northwest Atlantic (e.g., offshore islands), whereas some individuals from the Isle of May heavily relied on low-trophic-level terrestrial resources during breeding. However, it is important to note that our data from the breeding season represents the diet during the incubation period, when adults must feed only themselves. It is possible that Great Black-backed Gulls shift their diets during the chick-rearing period to higher trophic levels or more marine prey (Navarro et al., 2014).

Our study investigated the foraging ecology of Great Black-backed Gulls at both the population and individual levels, demonstrating the value of stable isotope analysis for understanding seabird diets beyond the breeding season (Calado et al., 2020; Ronconi et al., 2010). We contributed to growing evidence that trophic studies outside the breeding season are essential for a more complete understanding of species' ecology, and we showed that individual foraging strategies play an important role in shaping population-level patterns. Consistent with previous research, we found that Great Black-backed Gulls rely heavily on marine resources, contrasting with other often-sympatric *Larus* species that depend more on terrestrial resources (Lato et al., 2021; O'Hanlon et al., 2017; Ronconi et al., 2014; Steenweg et al., 2011). However, terrestrial resources may provide an important resource for Great Black-backed Gulls when competition for marine prey is high.

Seabird populations face a wide range of anthropogenic threats. The deterioration of marine ecosystems caused by environmental change and overfishing stand out as two of the main ones (Dias et al., 2019). The sustainable management of marine resources is therefore key for the preservation of functional marine food webs and, ultimately, for the conservation of seabird populations and other apex predators (Grémillet et al., 2018; Searle et al., 2023; Sherley et al., 2018). Trophic studies of seabirds play a crucial role in the identification of key resources that sustain seabird communities as well as other taxa (Harris et al., 2007; Hooker & Gerber, 2004). Our findings demonstrate that year-round trophic studies are required as an important step to better determine what resources seabirds rely on year-round, as there may be differences between the breeding and non-breeding period. Furthermore, quantifying individual-level foraging strategies—for example, enabling ecologists to determine the exposure of different subsets of individuals to specific threats, such as the deterioration of a habitat/resource or fisheries bycatch (e.g., Jiménez et al., 2016)—provides a better picture of how populations are structured in terms of individual resource use (Phillips et al., 2017).

CONCLUSION

We provide novel information about the foraging ecology of the Great Black-backed Gull, demonstrating that the way resources are exploited by generalist populations and individuals changes seasonally in response to the intrinsic and extrinsic pressures seabirds face during different times of the year. Therefore, it is important to undertake trophic studies beyond the breeding season to better understand species ecology during critical periods of seabird life history.

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Ethics

All procedures described in this study were approved by the relevant authorities: ethical approval obtained from the University of the Highlands and Islands; bird trapping, ringing, and feather clipping were carried out under permits from the BTO (permit #6690) and the BTO's Special Methods Technical Panel; and research licenses to carry out work on the Isle of May National Nature Reserve were obtained from NatureScot.

Author Contributions

SLL: Conceptualisation, Methodology, Validation, Formal analysis, investigation, Data curation, Writing – original draft, Writing – review and editing, Project administration. NJO: Conceptualisation, Methodology, Validation, Writing – review and editing, Supervision. JW: Conceptualisation, Validation, Writing – review and editing, Supervision. RM: Validation, Formal analysis, Data curation, Writing – review and editing. JW: Conceptualisation, Validation, Writing – review and editing, Supervision. FD: Conceptualisation, Validation, Writing – review and editing, Supervision. EAM: Conceptualisation, Methodology, Validation, Supervision, Writing – review and editing, Project administration, Funding acquisition.

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