

Annual and seasonal consistency in the feeding ecology of an opportunistic species, the yellow-legged gull *Larus michahellis*

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ABSTRACT: This study investigated the extent to which the plasticity of a generalist, opportunistic species allows individuals to shift their feeding ecology and foraging niche, throughout the annual cycle, and between 2 years of contrasting diet and oceanographic conditions during the breeding season. The spatio-temporal variations in the foraging niche of an overpopulated gull species—the yellow-legged gull *Larus michahellis* population at Berlenga Island (Portugal)—were assessed using blood (plasma and cells) and different feathers for stable isotope analyses ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) from 52 breeding adults in 2 consecutive years (2011 and 2012). In addition, GPS loggers were deployed on 11 individuals (and removed after several foraging trips) to infer the foraging behaviour of this species during the incubation period. Results suggest inter-annual differences in the feeding ecology and foraging behaviour of birds during the breeding season that were associated with the availability of food resources around the colony. Despite the high feeding plasticity and opportunistic behaviour of yellow-legged gulls, individual birds exhibited short- and long-term consistency in their feeding ecology, with exception of the period between winter and pre-laying. Our results support the hypothesis that individual feeding preferences throughout most of the annual cycle are an intrinsic characteristic of this population, and potentially of related opportunistic and generalist species.

KEY WORDS: Activity patterns · Generalist seabirds · Foraging specialization · Habitat use · GPS tracking · Stable isotopes

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INTRODUCTION

Foraging strategies of species can differ substantially, resulting in the exploitation of different niches. Of all seabird species, gulls *Larus* spp. are some of the most plastic, exploiting different habitats/resources (e.g. marine, coastal and terrestrial) and combining diet items of different origins (e.g. natural and anthropogenic sources) as demonstrated by several

studies (e.g. Villablanca et al. 2007, Moreno et al. 2009, Ramos et al. 2011). The generalist and opportunistic behaviour of most gull species allows individuals to modify their foraging strategies relatively easily (i.e. exploited habitat/resource, diet and spatial or temporal distribution) according, for instance, to the reproductive role or to the competition for food (Ramos et al. 2011, Ramírez et al. 2012). Inter-annual and seasonal variation of resources may influence

foraging and fitness of generalist and opportunistic species, such as gulls and skuas (Watanuki 1992, Votier et al. 2004, Sanz-Aguilar et al. 2009), which may have implications on individual specialization over time (individual consistency). Opportunistic species may owe their success to the fact that diet can change very quickly according to resource availability (Rutz & Bijlsma 2006, Ramírez et al. 2012), and therefore may have implications for the consistency of their diet and exploited habitat among seasons or contrasting years.

Flexibility in foraging is particularly relevant for populations of yellow-legged gull *Larus michahellis*, which have increased dramatically throughout Europe in recent decades. This increase has been mainly attributed to the ability of gulls to adapt to human-altered environments by opportunistically exploiting both terrestrial (e.g. refuse dumps) and marine (e.g. fishery discards) resources (Moreno et al. 2009, Ramos et al. 2009a). Previous studies have used diet (e.g. Munilla 1997, Ramos et al. 2009b, Matias & Catry 2010) and stable isotope analysis (SIA) (e.g. Moreno et al. 2009, Ramos et al. 2009a, 2011) to describe the feeding ecology of yellow-legged gulls. It is well documented that the pelagic Henslow's swimming crab *Polydora henslowii* is an important component of the diet of the yellow-legged gull (Moreno et al. 2009), which, despite its spatial and temporal unpredictability (Munilla 1997), may be the most important marine prey in Iberian Atlantic waters during the breeding season. Signa et al. (2008) suggested that the spatial structure of *P. henslowii* populations during the adult pelagic phase in coastal and surface waters in Galicia (Spain), as it gathers in shoals at high densities, is related to their feeding behaviour and oceanographic characteristics; the density of *P. henslowii* was positively correlated with chlorophyll *a* (chl *a*) and should be influenced by outwelling, upwelling and downwelling regimes.

Here, we tested for foraging consistency and investigated the foraging behaviour of yellow-legged gull breeding adults from Berlenga (the largest breeding colony of this species in Portugal) in 2 consecutive years (2011 and 2012) with markedly different baseline diet and oceanographic conditions. To our knowledge, this is the first study to provide tracking data for the yellow-legged gull. Together with conventional dietary sampling and individual movement data, multiple tissues with different turnover rates were sampled for SIA to test for spatio-temporal variation of resource exploitation along seasons and between years. By determining the isotopic composi-

tion ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) of blood (separated into plasma and cells) and feathers formerly grown during the summer and wintering seasons, we characterized feeding ecology during different periods of the annual cycle of the yellow-legged gull (Quillfeldt et al. 2010, Ramos et al. 2011). We evaluated short- (during breeding) and long-term (along seasons) consistency in the feeding ecology (trophic level and habitat/resource use) of yellow-legged gull individuals (Bearhop et al. 2006, Votier et al. 2010, Ceia et al. 2012). We expected low consistency in their feeding ecology, since they are very plastic and able to rapidly switch diet and habitat/resource use. Specifically, we predict that seasonal and inter-annual variation in food resources drive the (1) foraging niche and feeding ecology of the population, (2) short- and long-term consistency in the feeding ecology of individuals, and (3) foraging behaviour and effort of birds. Our goal was to investigate the extent to which the extreme plasticity of yellow-legged gulls allows individuals to respond to seasonal and, eventually, inter-annual variations during breeding and non-breeding periods.

MATERIALS AND METHODS

Study area and study species

Fieldwork was carried out during the incubation period of yellow-legged gulls during 2011 and 2012 at Berlenga Island, Portugal (39° 24' N, 009° 30' W). A large population of about 8500 pairs is estimated to breed in Berlenga Island, a small neritic island of ca. 78.8 ha about 11 km off the western Portugal coast. This island is situated within a large continental shelf characterized by shallow waters and high marine productivity due to coastal upwelling (Sousa et al. 2008). We selected chl *a* concentration (mg m^{-3}) and sea surface temperature (SST, °C) variables to characterize the marine environment used by yellow-legged gulls between years. Both environmental predictors were downloaded for a spatial resolution of 0.04° (approx. 4 km) of Aqua-MODIS mapped products from <http://coastwatch.pfeg.noaa.gov/coastwatch/CWBrowseWW180.jsp>. Mean composites of remote sensing data up to 100 km around the colony, from January to June in 2011 and 2012 (spatial and temporal scales that were relevant to characterize marine habitats based on the longest trip recorded and the temporal dynamism of these variables), were used to detect differences between years in the marine environment

used by the individuals during pre-laying and incubation periods. Chl *a* was \log_{10} transformed to fit a normal distribution. Monthly values of both variables were compared between years using a *t*-test followed by a Bonferroni correction. The presence of the pelagic crab *Polybius henslowii* in transects near the ocean surface was observed during 2 linear ship transects between Peniche and Berlenga Island (ca. 11 km) and 2 circular ship transects around Berlenga (ca. 5 km) in May and June of each year.

Sample collection

In May and June each year, 52 breeding adults (26 each year) with 3 egg clutches were trapped by setting square traps over their nests. Blood samples (0.5 to 1 ml from the tarsal vein) were collected from each bird using 27G needles and, within 2 to 3 h, separated into plasma and red blood cells (RBC) using a centrifuge (15 min at $1250 \times g$). The sampling scheme involved collecting 4 to 5 randomly selected breast feathers and the tips of the 1st primary (P1) and 8th secondary (S8), which were stored in sealed plastic bags for later SIA. Additionally, a GPS logger was deployed on 11 incubating birds (4 in 2011 and 7 in 2012) and removed after 3 to 25 foraging trips at sea (details of the devices below). Stomach contents were collected from 19 sampled individuals (5 in 2011 and 14 in 2012) by water-offloading, following Wilson (1984). Deployment or retrieval of devices and collection of samples took 10 to 15 min per bird.

Diet sampling and stable isotope analysis

All regurgitates came from breeding individuals. Each component (fish, crustaceans, refuse and terrestrial invertebrates) was sorted, and individual prey items identified to species-level whenever possible. The prey species identified in regurgitates collected from gulls were the fish species Atlantic horse mackerel *Trachurus trachurus* and blue whiting *Micromesistius poutassou*, and the pelagic crab *Polybius henslowii*. Refuse was represented by meat (chicken, beef scraps and organs from unknown species). We also found occasional terrestrial prey (terrestrial invertebrates) such as insects (bees and ants), spiders and snails. Fresh crustaceans (*P. henslowii*), fish (*T. trachurus* with otoliths attached; we were not able to collect fresh *Micromesistius poutassou*), refuse and terrestrial invertebrates were stored frozen for SIA.

Different tissues have different turnover rates and therefore can reflect temporal changes in trophic position and habitat/resource use (i.e. a change in isotopic niche; reviewed in Newsome et al. 2007). $\delta^{13}\text{C}$ values mainly reflect the habitat/resource use of consumers, while $\delta^{15}\text{N}$ values are mainly used to define the trophic position of consumers. Specifically, we analysed $\delta^{13}\text{C}$ (‰) and $\delta^{15}\text{N}$ (‰) in plasma, RBC, S8, P1 and breast feathers from each breeding adult sampled. Plasma and RBC retain information on diet from a few days prior to sample collection, up to the previous 3 to 4 weeks, as representative tissues of incubation and pre-laying period, respectively (Hobson & Clark 1993, Votier et al. 2010). Specific feathers provide isotopic information of a spatio-temporal period unrelated to the sampling period (Quillfeldt et al. 2010, Ramos et al. 2011); we collected P1 and S8 to represent the preceding summer and wintering seasons, respectively (Ramos et al. 2011), and breast feathers to represent the overall diet during the non-breeding season, because body feathers moult throughout the non-breeding season (Arcos et al. 2002). In addition, we analysed $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of fresh prey items obtained from stomach contents to create a basis for the interpretation of the isotopic signatures of tissues and further construction of mixing models (for further specifications on SIA methodology, see Appendix 1).

GPS tracking

During the 2 year study, 11 incubating adults were fitted with a GPS logger (CatTraq GT-120, Perthold Engineering LLC). The total mass of the device (17 g) was below 3% of adult mass (1.6 to 2.3%), as recommended by Phillips et al. (2003). The GPS loggers were attached to feathers in the mantle region with Tesa® tape, and set to record position (median error of <10 m) every 2 min, in order to have a detailed report of the gulls' movements. We tracked birds continuously from 2 to 8 d (median = 5 d), the data from which were used to determine 7 foraging behaviour and effort parameters (see 'Data analysis' below).

Data analysis

To estimate contributions for each dietary source to the diet of each individual, we adopted a Bayesian multi-source stable isotope mixing model (stable isotope analyses in R: SIAR; Parnell et al.

2010) under R 2.15.2 (R Development Core Team 2011, www.R-project.org). All possible combinations of each source contribution were examined using both isotope values ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) from plasma (corresponding to the incubation period) for each bird, and the mean and standard deviation of each of the 4 food sources collected from regurgitates (*Trachurus trachurus*, *Polybius henslowii*, refuse and terrestrial invertebrates). Isotopic data of *T. trachurus* were pooled, since no differences were found between 2011 and 2012 ($\delta^{13}\text{C}$: $F_{1,3} = 2.5$, $p = 0.21$; $\delta^{15}\text{N}$: $F_{1,3} = 0.8$, $p = 0.43$). For *P. henslowii*, we used the values from samples collected in 2012, because no crustaceans were found in the diet of gulls in 2011 (see results). Finally, we combined all items composed of refuse into a single category, and all terrestrial invertebrates into a distinct food source. There are no diet-blood fractionation factors available for yellow-legged gulls; hence, we used the average values of fractionation between prey and whole blood of 4 seabird species, from controlled experiments, available in the literature: 0.30 and 2.85‰ enrichment for carbon and nitrogen, respectively (Hobson & Clark 1992, Bearhop et al. 2002, Cherel et al. 2005a). A standard deviation of $\pm 1.0\%$ was adopted, considering potential differences in fractionation factors among species. SIA results were compared between years using an ANOVA or a Mann-Whitney *U*-test. To test the homogeneity of variances in both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, which provides a measure of niche width (see Bearhop et al. 2004 for more details), we used Levene's test. However, to analyse stable isotope data in the context of isotopic niche width between years and among seasons and periods, we adopted the recent metrics based in a Bayesian framework (Stable Isotope Bayesian Ellipses in R: SIBER; Jackson et al. 2011), which allows for robust statistical comparisons. The area of the standard ellipse (SEAc) was adopted to compare niche width between years, and a Bayesian estimate of the standard ellipse and its area (SEAB) to test whether group 1 is smaller than group 2 (i.e. *p*, the proportion of ellipses in 2011 that were lower than 2012; see Jackson et al. 2011 for more details). We used the computational code to calculate the metrics from SIBER implemented in the package SIAR (Parnell et al. 2010) under R 2.15.2.

To obtain an estimate of short-term consistency (between pre-laying and incubation periods) in carbon source and trophic level, stable isotope ratios in plasma were regressed with those in RBC. For long-term consistency, stable isotope ratios in RBC were regressed with those in S8 (between wintering sea-

son and pre-laying period), RBC with P1 (between summer season and pre-laying period) and S8 with P1 (between summer and wintering seasons). Since $\delta^{13}\text{C}$ has a trophic component, we used the residuals of the relationships with $\delta^{15}\text{N}$ in the same tissue categorised by year (2011 and 2012: plasma, RBC, S8 and P1; all $p < 0.05$) to determine the degree of repeatability in $\delta^{13}\text{C}$, independently of trophic effects (Bearhop et al. 2006, Votier et al. 2010, Ceia et al. 2012). We estimated correlation-based repeatability for Gaussian data to quantify the accuracy of these measurements using function 'rpt.corr' of the rptR package (nboot = 10 000, npermut = 10 000) under R 2.15.2. We used non-parametric bootstrapping and randomization tests to estimate the appropriate values of *r* (correlation coefficient) and *p* (significance testing), respectively (Nakagawa & Schielzeth 2010). Two outliers determined by visual inspection of the data that had a significant influence on the results for residual $\delta^{13}\text{C}$ in S8 and P1 in 2011 (−1.7 and −2.6, respectively) were excluded from these analyses. Based on these results, we were able to compare the consistency in foraging tactics of yellow-legged gulls between years and among seasons and periods.

The nonparametric fixed kernel density (FKD) estimator was used to calculate the 25, 50, 75 and 95% density contour areas of each trip using functions ('kernelUD', 'getvolumeUD', 'getverticeshr' and 'kernel.area') of the adehabitat package ($h = 0.05$, $grid = 500$; Calenge 2006) under R 2.15.2. GPS data-points at the colony were excluded from the analyses, and we defined foraging trips from the time the birds departed from the colony until their return. The overlap with land in the estimated foraging range was calculated based on the FKD.

Our measurements of foraging behaviour and effort comprised: (1) geographic position at maximum distance from the colony (latitude and longitude); (2) trip duration (hours); (3) maximum distance from colony (km); (4) trip length (km); (5) area covered (95% FKD; km^2); (6) number of trips per day; and (7) proportion of trips where birds foraged exclusively at sea. Variables (1) to (5) were calculated for each trip and compared between years creating variance components for ANOVA designs with random effects (mixed-ANOVA). The year was included as a fixed factor and bird identity as a random effect to control for pseudoreplication. Variables (6) and (7) were calculated per individual and compared between years with a Mann-Whitney *U*-test.

All data were tested for normality and homoscedasticity; trip duration was \log_{10} transformed,

maximum distance, trip length and area covered were square root transformed and proportions were arcsine transformed.

RESULTS

Diet and stable isotope analysis

Four food sources were collected from gull regurgitates in 2011 and 2012: fish, crustaceans, refuse and terrestrial invertebrates. The crustaceans (represented by *Polybius henslowii*) were not found in regurgitates of yellow-legged gulls in 2011, but occurred in 58.3% of the gull regurgitates containing food in 2012. Moreover, in 2011 we did not observe *P. henslowii* in gull pellets present in the colony, whereas in 2012 this species was extremely common in gull pellets. The transects performed by ship indicated a clear difference in presence of *P. henslowii* between 2011 and 2012: in 2011 we did not observe this species in the sea around the island, but in 2012 high densities shoals were common. These results indicate that *P. henslowii* was not consumed by gulls during the incubation period of 2011, possibly due to its absence or low densities. This pattern matched with monthly differences between years in the values of chl *a* and SST in a 100 km radius around the colony (*t*-test, Bonferroni correction: all $p < 0.01$). The significantly lower concentration of chl *a* in May 2011 than in May 2012 (*t*-test, Bonferroni correction: $p < 0.001$) and its abrupt decline from March to May 2011 contrasted with the pattern for 2012 (Fig. 1).

The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of the 4 food sources differed significantly (Kruskal-Wallis test; $\delta^{13}\text{C}$: $H_{3,18} = 9.6$, $p = 0.022$; $\delta^{15}\text{N}$: $H_{3,18} = 13.0$, $p = 0.005$) in at least one of the isotopes, with exception of *Polybius henslowii* and refuse (Table 1). However, differences were found in the homogeneity of their variances in both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ (Levene's test; $\delta^{13}\text{C}$: $F_{1,7} = 6.1$, $p = 0.042$; $\delta^{15}\text{N}$: $F_{1,7} = 52.4$, $p < 0.001$); the high variances in refuse indicate the wide isotopic spectrum of items ingested.

The SIAR mixing model outputs revealed significant differences between 2011 and 2012 in the relative proportion of food sources ingested. In 2012, the pelagic crab *Polybius henslowii* was the most consumed item (39.9%; Fig. 2). However, there was a significant decrease in the consumption of *Trachurus trachurus*, refuse and terrestrial invertebrates from 2011 to 2012 (45.1% to 34.4%, 38.2% to 12.3% and 16.7% to 13.4%; ANOVA; all $p < 0.001$).

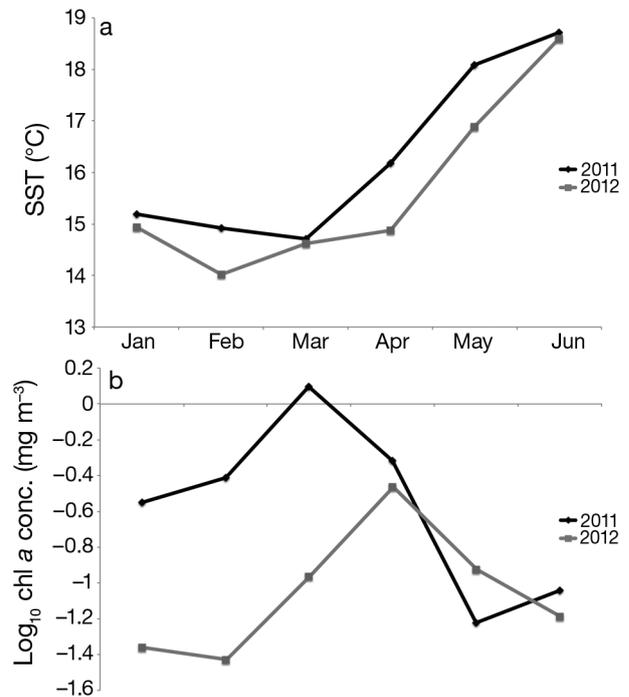


Fig. 1. Mean mensal composites of (a) Sea surface temperature (SST) and (b) \log_{10} chlorophyll *a* (chl *a*) concentration in 100 km radius around Berlenga Island, from January to June of 2011 and 2012

Table 1. *Larus michahellis*. Stable isotopic signature of carbon and nitrogen (mean \pm SD) of the 4 food sources recorded in regurgitates collected from incubating yellow-legged gulls at Berlenga Island. Terrestrial invertebrates included insects, spiders and snails

Prey source	n	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)
<i>Trachurus trachurus</i>	5	-18.6 ± 0.6	11.9 ± 0.6
<i>Polybius henslowii</i>	4	-17.8 ± 0.6	6.2 ± 0.2
Refuse	5	-17.1 ± 1.1	6.9 ± 4.3
Terrestrial invertebrates	4	-23.7 ± 4.0	15.2 ± 3.2

Inter-annual consistency in feeding ecology at the population level

The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of yellow-legged gulls' plasma (i.e. representing the incubation period), did not differ significantly between 2011 and 2012 (Mann-Whitney *U*-test; $\delta^{13}\text{C}$: $Z = -0.4$, $p = 0.65$; $\delta^{15}\text{N}$: $Z = 1.6$, $p = 0.11$). However, gulls exhibited substantial inter-annual differences in the homogeneity of variances in both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ (Levene's test; $\delta^{13}\text{C}$: $F_{1,50} = 5.0$, $p = 0.030$; $\delta^{15}\text{N}$: $F_{1,50} = 7.8$, $p = 0.007$), which provides a measure of niche width (see Bearhop et al. 2004). SIBER analysis revealed that niche width was twice as high in 2011, when yellow-legged gulls appar-

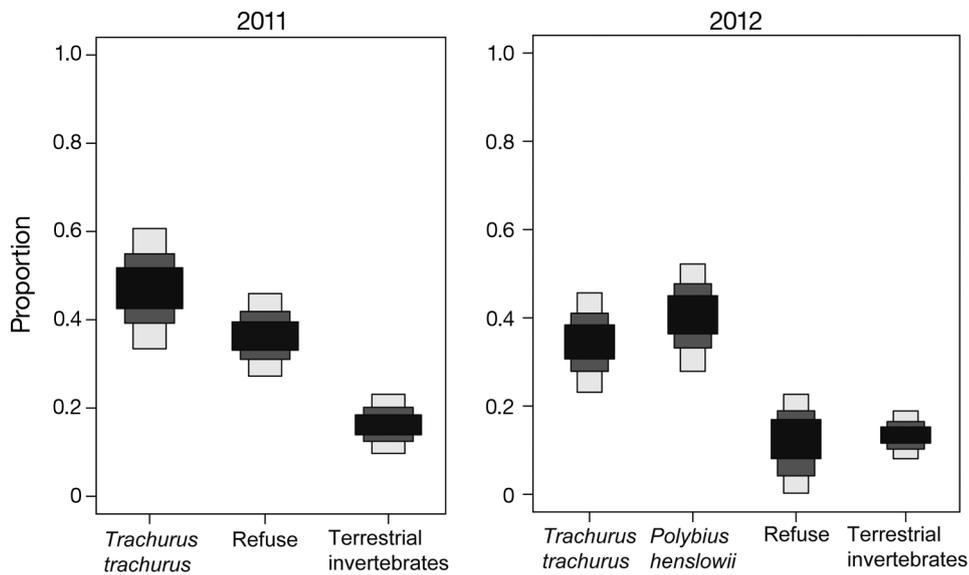


Fig. 2. *Larus michahellis*. Estimated proportions, based on C and N isotopic signatures of plasma, of the 4 main food sources in the diet of yellow-legged gulls from Berlenga Island during the incubation periods of 2011 and 2012. Terrestrial invertebrates included insects, spiders and snails. Decreasing bar widths represent 50, 75 and 95% Bayesian credibility intervals computed by Stable Isotope Analysis in R (SIAR; Parnell et al. 2010)

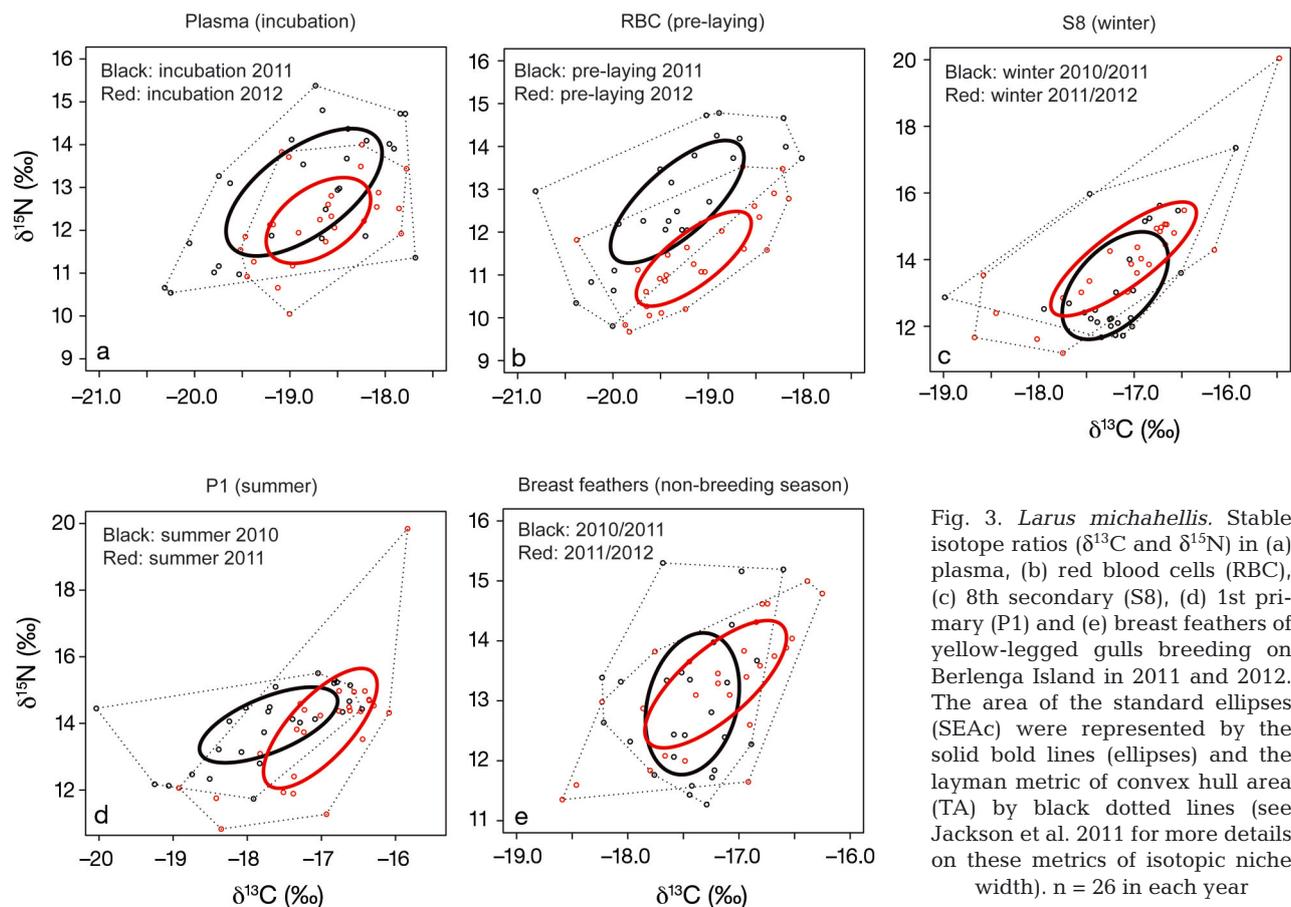


Fig. 3. *Larus michahellis*. Stable isotope ratios ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) in (a) plasma, (b) red blood cells (RBC), (c) 8th secondary (S8), (d) 1st primary (P1) and (e) breast feathers of yellow-legged gulls breeding on Berlenga Island in 2011 and 2012. The area of the standard ellipses (SEAc) were represented by the solid bold lines (ellipses) and the layman metric of convex hull area (TA) by black dotted lines (see Jackson et al. 2011 for more details on these metrics of isotopic niche width). $n = 26$ in each year

ently did not consume *Polybius henslowii* (SEA_B ; $p = 0.014$; Fig. 3a, see Appendix 2).

Significant differences between years were found for RBC (i.e. representing the pre-laying period) in $\delta^{15}\text{N}$ ($F_{1,50} = 14.6$, $p < 0.001$), but not in $\delta^{13}\text{C}$ ($F_{1,50} = 1.0$,

$p = 0.33$); in 2011, birds showed enrichment in $\delta^{15}\text{N}$ (Fig. 3b, Appendix 2). No differences between years were found for S8 (i.e. representing the winter season) in both $\delta^{13}\text{C}$ ($F_{1,50} = 0.2$, $p = 0.63$) and $\delta^{15}\text{N}$ ($F_{1,50} = 3.1$, $p = 0.08$) (Fig. 3c, Appendix 2). However,

there were significant differences between years for P1 (i.e. representing the summer season) in $\delta^{13}\text{C}$ ($F_{1,50} = 9.1$, $p = 0.004$), but not in $\delta^{15}\text{N}$ ($F_{1,50} = 0.1$, $p = 0.81$); birds showed depleted $\delta^{13}\text{C}$ values in the summer season of 2010 (Fig. 3d, Appendix 2). No differences were found between years for breast feathers (i.e. representing the non-breeding season) in both $\delta^{13}\text{C}$ (Mann-Whitney U -test; $Z = -1.8$, $p = 0.08$) and $\delta^{15}\text{N}$ ($F_{1,50} = 1.1$, $p = 0.29$) (Fig. 3e, Appendix 2). SIBER analyses did not reveal differences in niche width for any of these tissues (SEA_B; RBC: $p = 0.093$; S8: $p = 0.547$; P1: $p = 0.746$; breast feathers: $p = 0.461$).

Short- and long-term consistency in feeding ecology within a year

Similar patterns in short- and long-term consistency in feeding ecology of yellow-legged gulls were detected in both years. Strong significant positive relationships were found in $\delta^{15}\text{N}$ and in residual $\delta^{13}\text{C}$ (hereafter $\delta^{13}\text{C}$) between RBC and plasma of individual breeding adults in both years (Fig. 4a,b). These

results suggest short-term foraging consistency (in the pre-laying and incubation periods) within individuals in relation to both the use of the same habitat/resource and trophic level. In relation to longer-term consistency, significant relationships were found between P1 and RBC in $\delta^{15}\text{N}$ in both years (Fig. 4c), but not in $\delta^{13}\text{C}$, which suggests consistency in trophic level between the summer season and the pre-laying period. On the other hand, significant relationships were found between P1 and S8 in $\delta^{13}\text{C}$ in both years (Fig. 4d), but not in $\delta^{15}\text{N}$, which suggests consistency in habitat/resource use between the summer and the wintering seasons. Interestingly, no significant relationships were found in either $\delta^{15}\text{N}$ or $\delta^{13}\text{C}$ between S8 and RBC for either year.

Habitat selection and foraging behaviour

Overall, we documented 103 foraging trips from 11 individuals (2011: 25 trips from 4 individuals; 2012: 78 trips from 7 individuals). The spatial patterns of foraging habitat selection differed markedly

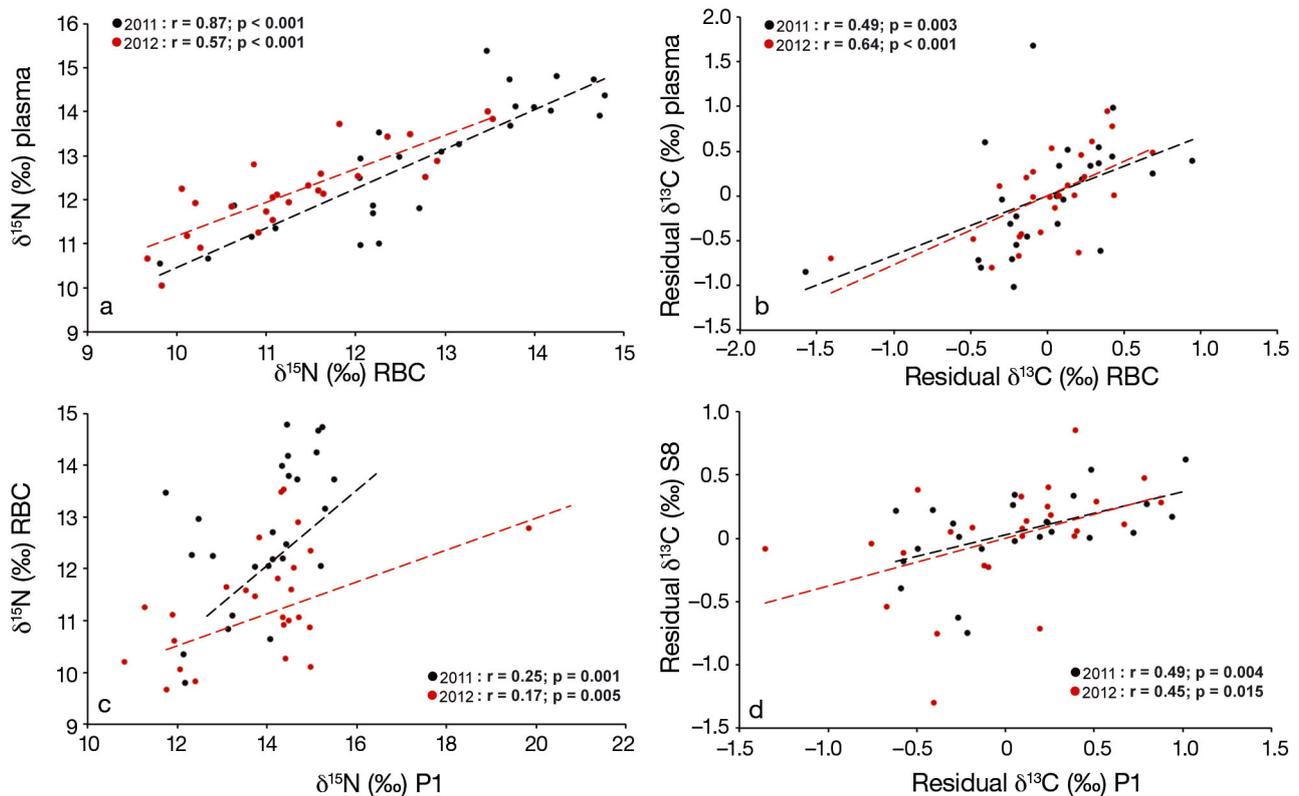


Fig. 4. *Larus michahellis*. Relationships between (a) $\delta^{15}\text{N}$ values in red blood cells (RBC) and plasma, (b) residual $\delta^{13}\text{C}$ values in RBC and plasma, (c) $\delta^{15}\text{N}$ values in 1st primary (P1) and RBC and (d) residual $\delta^{13}\text{C}$ values in P1 and 8th secondary (S8) of yellow-legged gulls breeding on Berlenga Island in 2011 and 2012. Values of r and p were estimated by correlation-based repeatabilities for Gaussian data (see Nakagawa & Schielzeth 2010)

Table 2. *Larus michahellis*. Comparison of foraging trip parameters performed by yellow-legged gulls from Berlenga Island during the incubation period in 2011 (25 foraging trips from 4 birds) and 2012 (78 foraging trips from 7 birds). Values are means \pm SD per individual, but statistical comparison was performed per trip using ANOVA (with year as a fixed effect and bird identity as a random effect), with the exception of trips per day and trips to the sea, in which a Mann-Whitney *U*-test was used. Significant results are in **bold**

	2011	2012	<i>F</i>	df	<i>p</i>
Max. latitude	39.35 \pm 0.13	39.38 \pm 0.03	0.2	1,9	0.704
Max. longitude	-9.33 \pm 0.06	-9.47 \pm 0.11	8.8	1,9	0.016
Trip duration (h)	7.0 \pm 1.4	3.6 \pm 2.6	6.7	1,9	0.030
Max. distance (km)	22.1 \pm 7.2	11.7 \pm 9.4	8.4	1,9	0.019
Trip length (km)	67.5 \pm 17.9	37.0 \pm 31.9	6.9	1,9	0.029
95 % FKD area (km ²)	751 \pm 119	337 \pm 314	9.6	1,9	0.013
	2011	2012	<i>Z</i>		<i>p</i>
Trips per day	1.1 \pm 0.2	2.6 \pm 2.3	-2.3		0.023
Trips to the sea (%)	22.9 \pm 20.8	75.2 \pm 35.7	-2.0		0.047

between 2011 and 2012. In 2012 birds preferred to forage at sea, whereas in 2011 they preferred to forage inland. The maximum longitude during trips was significantly different between years, but not latitude (Table 2), denoting inter-annual spatial segregation based on the type of habitat explored (marine vs. terrestrial). Birds used terrestrial and coastal habitats to forage in both years, such as refuse dumps (e.g. Leiria, Vilar, Azambuja and Rio Maior) and fisheries leftovers (e.g. Peniche harbour and Costa da Caparica seashore). However, the 25% FKD showed that the overlap with terrestrial habitat was 35.3% in 2011 and only 0.8% in 2012 (i.e. the overlap with Berlenga Island), which

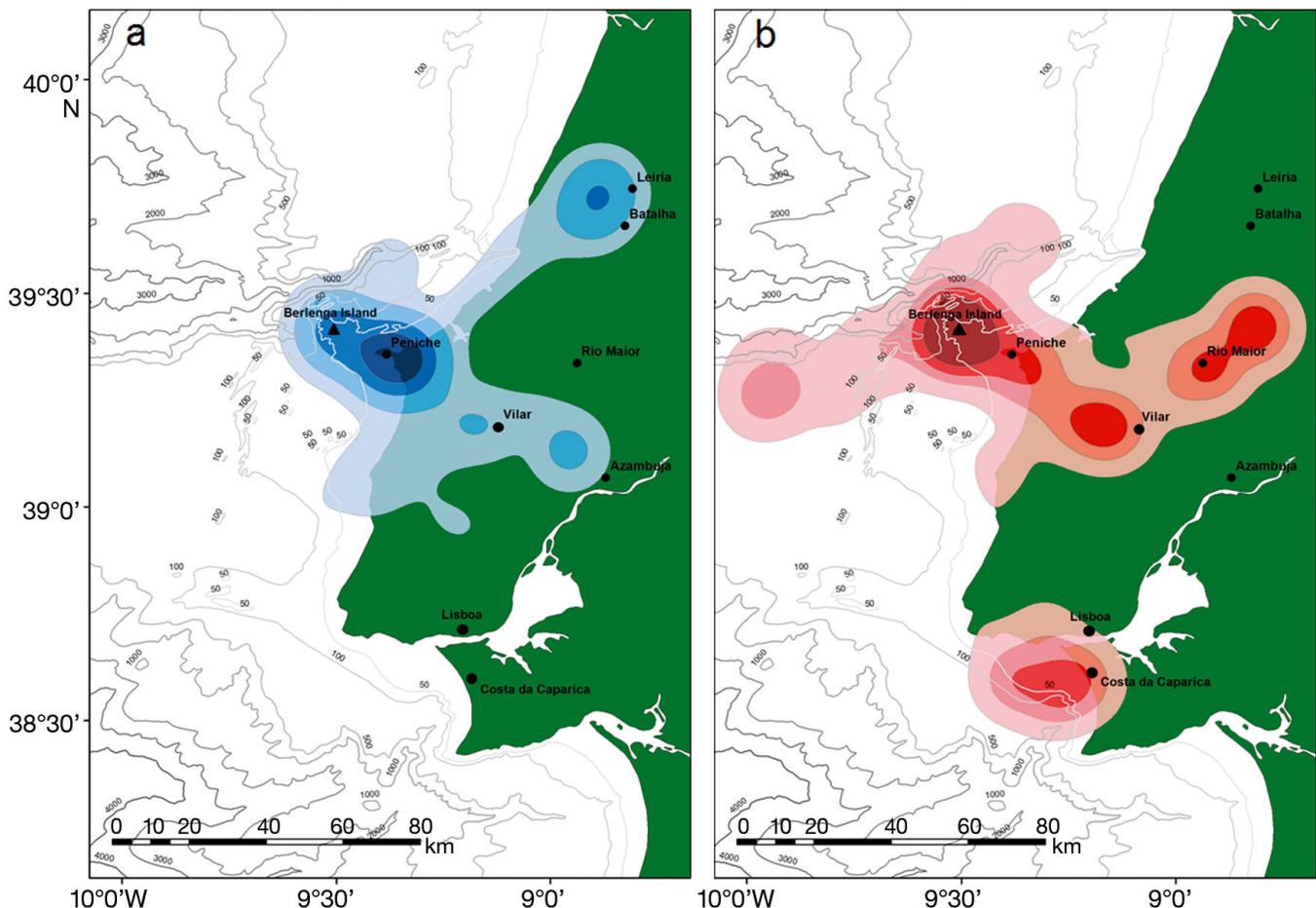


Fig. 5. *Larus michahellis*. Foraging distributions of yellow-legged gulls from Berlenga Island during the incubation period in (a) 2011 and (b) 2012. Decreasing kernel polygon shades represent 25, 50, 75 and 95% foraging home ranges

corresponded to the 2 feeding areas identified based on 25% FGD: (1) the area adjacent to the city of Peniche in 2011 (14 km from the colony; Fig. 5a), and (2) the marine area adjacent to the colony in 2012 (Fig. 5b).

Differences were found in the foraging behaviour and foraging effort of birds between years (Table 2). Specifically, the foraging trips were shorter (spatially and temporally), and the area covered by birds during foraging trips was significantly smaller in 2012 than in 2011. Differences were also found in the mean number of trips per day and in trips where individuals foraged exclusively at sea; both were significantly greater in 2012 than in 2011.

DISCUSSION

We used yellow-legged gulls as a model of a generalist and opportunistic species to infer consistency in feeding ecology at the population and individual levels in a small North Atlantic neritic island. Contrary to our expectations, our results show a high level of short- and long-term consistency in the feeding ecology of yellow-legged gulls at both the individual and population levels, in particular between some stages of their annual cycle (see below). The foraging behaviour, effort and niche width of yellow-legged gulls differed markedly between 2011 and 2012 during the incubation period, matching the strong variation in the oceanographic conditions and baseline diet between years during the same period. However, such differences between years had no major consequences for the overall patterns of short- and long-term consistency in the feeding ecology of individuals.

The significantly lower concentration of chl *a* in May 2011 than in May 2012 (i.e. during the incubation period) and its abrupt decline from March to May 2011 contrasted with the pattern for 2012, and matched the apparent absence of Henslow's swimming crab *Polybius henslowii* in 2011. Our results suggest that the absence of *P. henslowii* from the diet of incubating yellow-legged gulls at Berlenga during 2011 was likely related to adverse oceanographic conditions around the island, which could influence the availability of this species as suggested by Signa et al. (2008). The SIAR mixing model revealed high significant differences in the relative proportion of the 4 main food sources in the diet of yellow-legged gulls between 2011 and 2012. Because *P. henslowii* and refuse lacked differences in both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, SIAR could not precisely differentiate their relative proportions. However, due to its distinct origin and

importance to the yellow-legged gulls' diet, both food sources were considered independently as their homogeneity of variances differed significantly in both isotope ratios.

Yellow-legged gulls showed inter-annual differences in feeding ecology during both the incubation and pre-laying periods. A significantly higher isotopic niche width in 2011 than 2012 (twice higher), and inter-annual differences in the homogeneity of variances in both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in plasma were detected during the incubation period. The broad spectrum of trophic levels in refuse and the small variances in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of *Polybius henslowii* appeared to be the basis of these differences, because populations with individuals consuming prey over a narrow spectrum of trophic levels will tend to show less isotopic variance than those feeding on a broad spectrum of items from different trophic levels (Bearhop et al. 2004). During the pre-laying period, inter-annual differences were found in the occupancy of the isotopic niche — mainly driven by greater significant $\delta^{15}\text{N}$ values in 2011 — but no differences were found in the niche width. We have no data to corroborate the diet of yellow-legged gulls during the pre-laying period, but our results suggest a diet shift during this period between 2011 and 2012. On the other hand, no differences were found in the feeding ecology of yellow-legged gulls during the non-breeding season between years. Inter-annual differences in habitat/resource use, but not in trophic level, were detected at the population level during the summer season (i.e. in P1; Ramos et al. 2011). However, these differences vanished during the non-breeding season, and in the winter season yellow-legged gulls exhibited a similar foraging niche between years. Since breeding birds are confined to a limited foraging area around the colony, foraging opportunities should be more limited during the breeding than during the non-breeding season (Ramos et al. 2011).

Correlations in stable isotope ratios between different tissues can highlight particular details of seabird ecology, such as the degree of foraging specialization (Bearhop et al. 2006, Votier et al. 2010, Ceia et al. 2012). The yellow-legged gull is widely considered to be a generalist top predator, but our results document short- and long-term consistency in feeding ecology within individuals along seasons in 2 consecutive years. Furthermore, a similar pattern in the consistency levels was found between 2011 and 2012, despite their strong different patterns in prey consumption and oceanographic conditions during the breeding season. Specifically, we detected (1) a high level of short-term consistency within individuals in the feeding ecology (i.e. in habitat/resource use and

in trophic level) between the pre-laying and the incubation periods; (2) long-term consistency in trophic level between the summer season and the pre-laying period; and (3) long-term consistency in habitat/resource use between the summer and the wintering seasons. These results suggest individual preferences in the feeding ecology of this highly opportunistic and generalist species at specific stages of its annual cycle. Therefore, this characteristic may be widespread in this population and related species, and could be driven mostly by traits affecting the individual (e.g. individual specialization, intra-specific competition) rather than by traits affecting the whole population (e.g. environmental conditions), as demonstrated in other species such as penguins (e.g. Cherel et al. 2007), albatrosses (e.g. Ceia et al. 2012), guillemots (e.g. Woo et al. 2008), gannets (e.g. Votier et al. 2010) and skuas (e.g. Anderson et al. 2009). However, greater variation within individuals than among individuals from the winter season to the pre-laying period — as no relationships were found between S8 and RBC for either of the 2 years — strongly suggests that the general feeding pattern changed within the population. These results are in accordance with Ramos et al. (2011), who reported a change in dietary preferences between the non-breeding and breeding seasons for the same species in the Mediterranean. However, our study suggests that strong changes in the feeding ecology of the whole breeding population occur from the winter season to the pre-laying period.

Although the sample size of tracked birds was relatively low in both years, our results suggested substantial inter-annual variation in foraging behaviour and effort of yellow-legged gulls during the incubation period on Berlenga Island. There were differences in both spatial and temporal patterns of the trips, and in their frequency. Apparently, this variability was strongly related to the gulls' diet, which differed markedly between the 2 years. Our results suggest that foraging behaviour of this opportunistic species is influenced to a large extent by prey conditions around the colony. Similarly, Schwemmer et al. (2013) found that the foraging behaviour of lesser black-backed gulls *Larus fuscus* in the North Sea was influenced by the availability of swimming crabs *Liocarcinus* spp. around the colony.

CONCLUSIONS

As expected, our study confirms that the opportunistic and generalist behaviour of yellow-legged gulls permits individuals to respond to seasonal and

inter-annual variations in resources, during both the breeding and non-breeding seasons, by exploiting different foraging niches. Inter-annual changes in baseline diet during the breeding season, likely due to the absence of the prey crab *Polybius henslowii* at sea around the colony, influenced variation in niche width and foraging behaviour of the yellow-legged gull population. Results suggest that birds gradually changed their feeding behaviour throughout the year according to extrinsic factors, such as the available resources, and intrinsic factors, such as individual preferences. However, they showed an abrupt change in feeding ecology at the population level between winter and the pre-laying period, suggesting that this last period is the most susceptible in their annual cycle. Yellow-legged gulls showed high short-term consistency in feeding ecology during the breeding season, and long-term consistency in trophic level and habitat/resource use between seasons. Similar patterns of individual consistency were found in both study years, thus highlighting individual feeding preferences in the ecological role of this opportunistic species.

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Appendix 1. Preparation of the tissue samples for stable isotope analyses (SIA) and determination of nitrogen and carbon isotope ratios

Samples (plasma, RBC and prey items) were freeze-dried and homogenized prior to SIA. Because high lipid concentrations in plasma and in flesh from prey items can lead to depleted $\delta^{13}\text{C}$ values, lipids were removed using successive rinses in a 2:1 chloroform-methanol solution (Cherel et al. 2005b). Prior to SIA, feathers were cleaned of surface contaminants using successive rinses in a 2:1 chloroform-methanol solution, dried at 60°C for 24 h and then homogenized. The carbon and nitrogen isotopic composition of the samples were determined using a Flash EA1112 Series elemental analyser coupled on line via Finnigan conflo II interface to a Thermo Delta V S mass spectrometer. Approximately 0.3 mg of each sample was combusted in a tin cup for the simultaneous determination of nitrogen and carbon isotope ratios. Isotope ratios are presented in the usual δ notation based on the PeeDee Belemnite (PDB) for carbon and atmospheric N_2 (AIR) for nitrogen, and expressed as ‰. $\delta^{13}\text{C}$ or $\delta^{15}\text{N} = [(R_{\text{sample}} / R_{\text{standard}}) - 1] \times 1000$, where $R = {}^{13}\text{C}/{}^{12}\text{C}$ or ${}^{15}\text{N}/{}^{14}\text{N}$, respectively. Replicate measurements of internal laboratory standards (acetanilide) indicate precision <0.2‰ for both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$.

Appendix 2. Niche width context

Stable isotope ratios of carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) in plasma, red blood cells (RBC), 8th secondary (S8), 1st primary (P1) and breast feathers of yellow-legged gulls *Larus michahellis* breeding on Berlenga Island in 2011 (n = 26) and 2012 (n = 26). The area of the standard ellipse (SEAc) and the layman metric of convex hull area (TA) are also shown (see Jackson et al. 2011 for more details on these metrics of isotopic niche width). Values are means \pm SD (min.; max.)

Tissue type	$\delta^{13}\text{C}$ (‰)		$\delta^{15}\text{N}$ (‰)		SEAc		TA	
	2011	2012	2011	2012	2011	2012	2011	2012
Plasma	-18.9 ± 0.8 (-20.3; -17.7)	-18.7 ± 0.5 (-19.5; -17.8)	12.9 ± 1.5 (10.5; 15.4)	12.2 ± 1.0 (10.0; 14.0)	3.03	1.51	8.09	4.60
RBC	-19.3 ± 0.7 (-20.8; -18.0)	-19.2 ± 0.6 (-20.4; -18.2)	12.7 ± 1.4 (9.8; 14.8)	11.4 ± 1.1 (9.7; 13.5)	2.18	1.39	7.28	4.69
S8	-17.2 ± 0.5 (-19.0; -15.9)	-17.1 ± 0.7 (-18.7; -15.5)	13.2 ± 1.6 (11.7; 17.4)	14.0 ± 1.7 (11.2; 20.0)	2.43	2.41	8.06	10.75
P1	-17.7 ± 0.9 (-20.0; -16.5)	-17.0 ± 0.8 (-18.9; -15.8)	14.0 ± 1.1 (11.7; 15.5)	13.9 ± 1.8 (10.8; 19.8)	2.59	2.99	8.25	11.91
Breast feathers	-17.4 ± 0.4 (-18.2; -16.6)	-17.2 ± 0.6 (-18.6; -16.3)	13.0 ± 1.2 (11.3; 15.3)	13.3 ± 1.0 (11.4; 15.0)	1.52	1.45	4.51	4.44

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