Mar Biol (2014) 161:1861–1872
DOI 10.1007/s00227-014-2468-9

ORIGINAL PAPER

Can variations in the spatial distribution at sea and isotopic niche width be associated with consistency in the isotopic niche of a pelagic seabird species?

Filipe R. Ceia · Vitor H. Paiva · Stefan Garthe · João C. Marques · Jaime A. Ramos

Received: 14 November 2013 / Accepted: 21 May 2014

Abstract This study tested for fluctuations on short-term consistency (within about 1 month) in the isotopic niche of a pelagic seabird species. Short-term consistency in the isotopic niche was assessed using a wide-ranging apex predator, the Cory's shearwaters *Calonectris diomedea*, along a 3-year study (2010–2012), during both the pre-laying and chick-rearing periods, with markedly inter- and intra-annual differences in the foraging spatial distribution at sea and isotopic niche width. We used individual movement data and stable isotope data, analysed using recent metrics based in a Bayesian framework, of 69 adults breeding on a small neritic island in the North Atlantic (39°24′N, 009°30′W). As expected, our results confirm that isotopic niche expansion could arise via increased variation in spatial distribution at sea among individuals. Results suggest fluctuations on short-term consistency in the isotopic niche of Cory's shearwaters related to their different foraging patterns among periods and, ultimately, to presumably temporal changes in the availability and predictability of food resources. Short-term consistency in the isotopic niche was higher and persistent during periods when the population showed an intermediate isotopic niche width and absent when isotopic niche was either smaller or larger during the study period. These results suggest that consistency in the isotopic niche is an important characteristic of this population during the breeding period that may fluctuate depending on resources availability and should be important to understand the dynamics of foraging ecology of pelagic seabirds in general.

Introduction

The ecological niche of a population is a fundamental concept in ecology, but there are several niche concepts, each of which emphasizing a different aspect of a species' ecological characteristics (see Newsome et al. 2007 for a review). In terms of diet, generalist populations typically exhibit higher niche variation than more specialized populations due to a higher degree of diet variation (Van Valen 1965; Bolnick et al. 2007), which can arise within a single population via foraging plasticity among its individuals, resulting in resource use diversity (Svanbäck and Bolnick 2007). Foraging strategies of individual birds can differ substantially, and individuals of the same species may use different resources (Weimerskirch et al. 2005), resulting in the exploitation of different niches, which could be consistent within individuals over time (see Bolnick et al. 2003 for a review). Accordingly, there has been a recent increase in studies of individual consistency in the foraging niche within populations (e.g. Bearhop et al. 2006; Votier et al. 2010), suggesting that some individuals have a narrow foraging niche (i.e. individuals use a subset of their population's niche), helping to reduce intra-specific competition (Svanbäck and Bolnick 2007; Matich et al. 2011; Ceia et al. 2012). Fluctuations on consistency in the foraging niche at the individual level have been described in species such as perches *Perca fluviatili* (Svanbäck and Persson 2004), sea otters *Enhydra lutris* (Tinker et al. 2008)

Communicated by Y. Cherel.

F. R. Ceia (✉) · V. H. Paiva · J. C. Marques · J. A. Ramos
Department of Life Sciences, Marine and Environmental Research Centre (IMAR/CMA), University of Coimbra, 3004-517 Coimbra, Portugal
e-mail: ceiafilipe@zoo.uc.pt

S. Garthe
Research and Technology Centre (FTZ), University of Kiel, 25761 Büsum, Germany

and Brünnich's guillemots *Uria lomvia* (Woo et al. 2008), apparently related to temporal changes in the predictability of resources, although Ceia et al. (2014) did not found apparent fluctuations on consistency of yellow-legged gulls *Larus michahellis* between 2 years of contrasting diet and foraging patterns despite their high consistency in the feeding ecology. Here, we expect to assess inter-annual and seasonal variation in the consistency of isotopic niche (as a proxy of foraging niche) of a pelagic seabird species, the Cory's shearwaters *Calonectris diomedea borealis*.

During the breeding season, Cory's shearwaters are central place foragers capable of travelling distances up to 5,500 km (Magalhães et al. 2008) in a single foraging trip. Such long trips, however, are more expected in oceanic (i.e. typically lower productive regions) than in neritic (i.e. typically higher productive regions) areas, because of higher prey patchiness and prey distribution along the neritic-oceanic marine productivity gradient (Paiva et al. 2010). Similarly, longer trips are relatively more frequent during the early stages of the breeding season, pre-laying and incubation periods, than during later stages, the chick-rearing period, when birds must forage within a shorter range in order to provide food for their chicks (Paiva et al. 2010, 2013b), which is mainly composed on fish and cephalopods (Xavier et al. 2011; Neves et al. 2012). Recent studies demonstrated relationships between geographic locations and stable isotope signatures for marine predators (e.g. Cherel and Hobson 2007; Phillips et al. 2009; Jaeger et al. 2010); thus, we should expect that a higher variation in the foraging spatial distribution among individuals from the same population would lead to a wider isotopic niche of such population. Given their wide range in foraging patterns according to the breeding stage, prey abundances and oceanographic conditions (Paiva et al. 2013a), Cory's shearwaters are a good model species to evaluate spatial variations at sea and isotopic niche width and investigate for fluctuations on consistency in the isotopic niche within and among individuals. Concurrently, foraging niche of a population is poorly studied, particularly concerning pelagic seabirds. Classical tools (e.g. conventional dietary analyses and census at sea) have been widely used to describe the foraging niche of pelagic seabirds but an accurate assessment of spatial distribution at sea and trophic ecology of seabirds only recently was possible through the use of recent technology such as tracking devices and stable isotope analyses (e.g. Weimerskirch et al. 2002; Bearhop et al. 2004; Cherel et al. 2005b).

In this study, we used individual movement data (GPS tracking) and isotopic signature ($\delta^{13}C$ and $\delta^{15}N$) from blood of Cory's shearwater breeding adults, separated into plasma and cells, to evaluate short-term consistency (within about 1 month) in the isotopic niche of individuals along 3 years (2010–2012), during both the pre-laying and chick-rearing periods. We tested for fluctuations on short-term consistency in the isotopic niche of individuals among years and between breeding periods with markedly different foraging patterns. Specifically, we predicted fluctuations in short-term consistency in the isotopic niche of Cory's shearwaters within a population, since they are able to show large variations in spatial distribution at sea and isotopic niche width.

Materials and methods

Fieldwork was conducted in Berlenga Island, Portugal (39°24′N, 009°30′W), during the pre-laying (April–May) and chick-rearing (August–September) periods of Cory's shearwaters along 2010, 2011 and 2012. A population of about 1,000 breeding pairs of Cory's shearwaters is estimated to breed in Berlenga Island, a small neritic island of ca. 78.8 ha, and adjacent rocky islets (Lecoq et al. 2011), 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 the coastal upwelling that lasts from April to September (Sousa et al. 2008).

Sample collection

A total of 69 breeding adults were sampled along 2010, 2011 and 2012 (pre-laying period: five males and 5 females, 7 males and 1 female, 11 males and 1 female, respectively; chick-rearing period: 9 males and 10 females, 8 males and 3 females, 7 males and 2 females, respectively). Repeated measures of 17 individuals were performed in different seasons, but all birds were sampled only once within a season to avoid overlap between the sampling events. A GPS logger was deployed on each bird and removed after 1–18 foraging trips at sea (details of the devices below). Blood samples (0.5–1 ml from the tarsal vein) were collected from each bird on recapture using 27G needles and, within 2–3 h, separated into plasma and red blood cells (RBC) using a centrifuge (15 min at 2,910 g). Haematocrit was recorded as the proportion of RBC in total blood volume, and samples were then stored frozen until preparation for stable isotope analyses. Captured birds were ringed, and wing and tarsus-lengths were measured and weighed both on capture and recapture. In addition, a total of 65 nests including the nests of all sampled birds were monitored twice, in May and late September, to determine laying and fledging success, respectively. Deployment or retrieval of devices and collection of blood samples took 10–15 min, and birds were returned immediately to their nest.

Tracking data collection

Each individual bird was fitted with a GPS logger (CatTraq GT-120, Perthold Engineering LLC). The plastic case was removed and replaced by a 7-cm-long thermo-retractile rubber sleeve reducing the total weight to 17 g. This corresponded to 1.7–2.6 % of studied individuals' mass, which is below the recommended 3 % threshold reported to have no deleterious effects on seabird species during short-term (Phillips et al. 2003; but see Vandenabeele et al. 2012), including Cory's shearwaters (Igual et al. 2005). 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 5 min. Birds locations were recorded continuously from 1 to 19 days (10.3 ± 4.7 days).

Stable isotope analyses (SIA)

Stable isotope analyses of carbon and nitrogen were performed to estimate and compare isotopic niche width among years and between periods (Bearhop et al. 2004; Newsome et al. 2007; Jackson et al. 2011). Carbon stable isotope value ($\delta^{13}C$) mainly reflects the carbon source (food and habitat type) of consumers, while nitrogen stable isotope value ($\delta^{15}N$) is mainly used to define trophic position of consumers (Newsome et al. 2007). Plasma and RBC retain information on diet from a few days prior to sample collection (hence, plasma reflects choices made during the tracking period), up to the previous 3–4 weeks, respectively. Because of the differing turnover rates of plasma and RBC, we were able to investigate the effect of short-term consistency in the isotopic niche (Votier et al. 2010; Ceia et al. 2012). We analysed $\delta^{13}C$ (‰) and $\delta^{15}N$ (‰) in plasma and RBC from each breeding adult sampled and tracked. Samples were freeze-dried and homogenized prior to SIA. Because high lipid concentrations in plasma can lead to depleted ^{13}C values, lipids were removed using successive rinses in a 2:1 chloroform–methanol solution (Cherel et al. 2005a). We did not control for possible changes in plasma $\delta^{15}N$ values after lipid extraction; lipid extraction generally does not affect plasma $\delta^{15}N$ values (Cherel et al. 2005b), although some studies reported slight differences (both increased and decreased values) after lipid removal in whole blood (Bearhop et al. 2000; Cherel et al. 2005a). Hence, plasma $\delta^{15}N$ values in the present study might be somewhat over- or sub-estimated. Nitrogen and carbon isotope values were determined via Finnigan conflo II interface to a Thermo Delta V S mass spectrometer coupled to a Flash EA1112 Series elemental analyser using analysis of acetanilide STD (Thermo scientific-PN 338 36700) as a calibration standard. Approximately 0.3 mg of each sample was combusted in a tin cup for the simultaneous determination of nitrogen and carbon isotope values. Stable isotope values are present in the usual δ notation based on the Pee-Dee Belemnite (PDB) for carbon and atmospheric N_2 (Air) for nitrogen and expressed as ‰. $\delta^{13}C$ (‰) or $\delta^{15}N$ (‰) $= [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1{,}000$, where $R = {}^{13}C/{}^{12}C$ or $^{15}N/^{14}N$, respectively. Long-term performance of the mass spectrometer was monitored by analysis of secondary isotopic reference material (acetanilide STD: C and N contents of 71.09 and 10.36 %, respectively) in every batch, indicating precision <0.2 ‰ for both $\delta^{13}C$ and $\delta^{15}N$.

Breeding success and bird condition status

We determined laying success (number of eggs laid/number of nests) and breeding success (number of fledged birds/number of eggs laid) of Cory's shearwaters, as proxies of breeding condition among years. The standard residuals of the relationship between body mass (mean between capture and recapture) and tarsus length ($F_{1,67} = 104.1$, $P < 0.001$, $r = 0.598$) were used to estimate body mass index of all sampled birds, an index primarily reflecting body lipid reserves (Sánchez-Guzmán et al. 2004), to evaluate whether breeding adults were in a similar body condition. In addition, the haematocrit was calculated, which in conjunction with other physiological indicators such as body mass index, can be a useful indicator of the current condition status of the individuals (see Fair et al. 2007 for a review).

Data analysis

GPS data were separated into individual foraging trips by calculating the time from when the birds departed the colony until their return. GPS locations at the colony were excluded from analyses. Then, the relocations (between consecutive tracking points) were divided into search flights and active feeding versus travelling according to flight speed; according with Louzao et al. (2009), we only used GPS relocations, which exclusively represented the areas where Cory's shearwaters were searching for food (10–15 km h^{-1}) and active feeding (2–10 km h^{-1}). Finally, a distance-to-colony filter of 2 km was applied, to remove relocations while flying over the colony before landing.

The nonparametric fixed kernel density (FKD) estimator was used to calculate the 25, 50 and 75 % density contour areas (km^2), of each bird using functions ("*kernelUD*", "*getvolumeUD*", "*getverticeshr*" and "*kernel.area*") of the *adehabitat* package ($h = 0.18°$, $grid = 500$ m; Calenge 2006) under R 2.15.2 (R Development Core Team 2011). The intra-specific overlap in the estimated foraging range among individuals within each period was assessed following Fieberg and Kochanny (2005). The 25, 50 and 75 % FKD overlaps were calculated for each bird using the function "*kerneloverlap*" of the *adehabitat* package (*meth* = "VI"; Calenge 2006) under R 2.15.2. We also determined the maximum distance from colony (km) and geographic position at maximum distance from the colony (latitude and longitude) of each bird to investigate the effect of latitude, longitude and foraging range on isotopic niche.

To analyse stable isotope data in the context of isotopic niche among the periods, we adopted the recent metrics based in a Bayesian framework that allows robust comparison to be made among data sets comprising different sample sizes (Stable Isotope Bayesian Ellipses in R: SIBER; Jackson et al. 2011; but see Syvaranta et al. 2013). The standard ellipse area corrected for small sample sizes (SEAc, an ellipse that contains 40 % of the data regardless of sample size) was adopted to compare niche width among years and between periods (see Jackson et al. 2011 for more details). The Bayesian approximation of the standard ellipse area (SEAb) and the layman metric of convex hull area (TA; Layman et al. 2007) were also calculated as a measure of isotopic niche area, following Jackson et al. (2011). We used the computational code to calculate the metrics from SIBER using functions ("*standard.ellipse*", "*siber.ellipses*" and "*convexhull*") implemented in the package SIAR (stable isotope analyses in R: SIAR; Parnell et al. 2010) under R 2.15.2.

All foraging variables and SIA results were compared among periods using a Kruskal–Wallis test followed by multiple comparisons. To test for homogeneity of variances in both δ^{13}C and δ^{15}N, which provides a measure of trophic niche width (see Bearhop et al. 2004 for more details), we used a Levene's test. Similarly, a Levene's test was used to test for the assumption of equal variances in foraging variables (25, 50 and 75 % FKD and maximum distance from colony) as a measure of variation in foraging patterns. We only used individuals for which we have collected the essential information (tracking data and SIA simultaneously), to fulfil our objectives of focusing on the variability at individual level and not at the population level. Thus, although the sample size in each sampling period (between 8 and 19 birds) could not provide reliable estimates of total home-range area and isotopic niche width of the whole population in each period (see Syvaranta et al. 2013; Soanes et al. 2013), it should have a minor influence on the assessment of variability in isotopic niche and spatial distribution at sea on the studied individuals in different periods (see Layman et al. 2007).

To obtain an estimate of short-term consistency in carbon source and trophic level, we regressed stable isotope values in plasma on those in RBC (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 randomization tests to estimate the appropriate value of p (significance testing) for each regression (Nakagawa and Schielzeth 2010). Based on these results, we were able to evaluate short-term consistency in isotopic niche (i.e. shifts in trophic level and carbon source) in the different periods and tested for fluctuations in consistency presumably associated with spatial distribution at sea and isotopic niche width during the study period.

All data were tested for normality and homoscedasticity; foraging area (25, 50 and 75 FKD) and maximum distance from the colony were $\log_{10}$-transformed to assess relationships among the six studied periods, and proportions were arcsine transformed. When transformation did not normalize the data, nonparametric tests were used. Values are presented as mean ± SD.

Results

Spatial distribution at sea

From 2010 to 2012, we documented a total of 394 foraging trips by 69 individuals. The longest trip recorded in terms of duration was 19 days during the 2012 pre-laying period and the farthest trip distanced 3,236 km from the colony (trip length = 7,135 km) during the 2011 pre-laying period (Fig. 1). Although birds explored a larger area (25, 50 and 75 % FKD) during the pre-laying period than during the chick-rearing period in both 2011 and 2012, differences among all periods were only significant at 75 % FKD (Kruskal–Wallis test: $H_{5,69} = 12.2$, $P = 0.033$). During the 2011 pre-laying period, birds visited a larger area at 75 % FKD and showed highly significant differences in foraging trips at maximum distance from the colony and in longitude (see Table 1 for multiple comparisons). However, highly significant differences in the homogeneity of variance for areas explored among all periods at 25, 50 and 75 % FKD (Levene's test: all $P < 0.01$) indicate wide range of variances in the foraging area among the six periods, with a particularly high variance for the 2011 pre-laying period (Table 1). Differences were also found in the overlap in the estimated foraging areas at 25, 50 and 75 % FKD among all periods (Kruskal–Wallis test: all $P < 0.01$); specifically, the overlap among birds within each period was significantly greater during the 2012 chick-rearing period than in any other period for any percentage (25, 50 and 75 % FKD) of overlap (Table 1).

Isotopic niche width

The δ^{13}C and δ^{15}N of Cory's shearwaters' plasma, which provides an indication of recent meals (i.e. during the tracking period), differed significantly among all periods (Kruskal–Wallis test: all $P < 0.01$), with overall higher

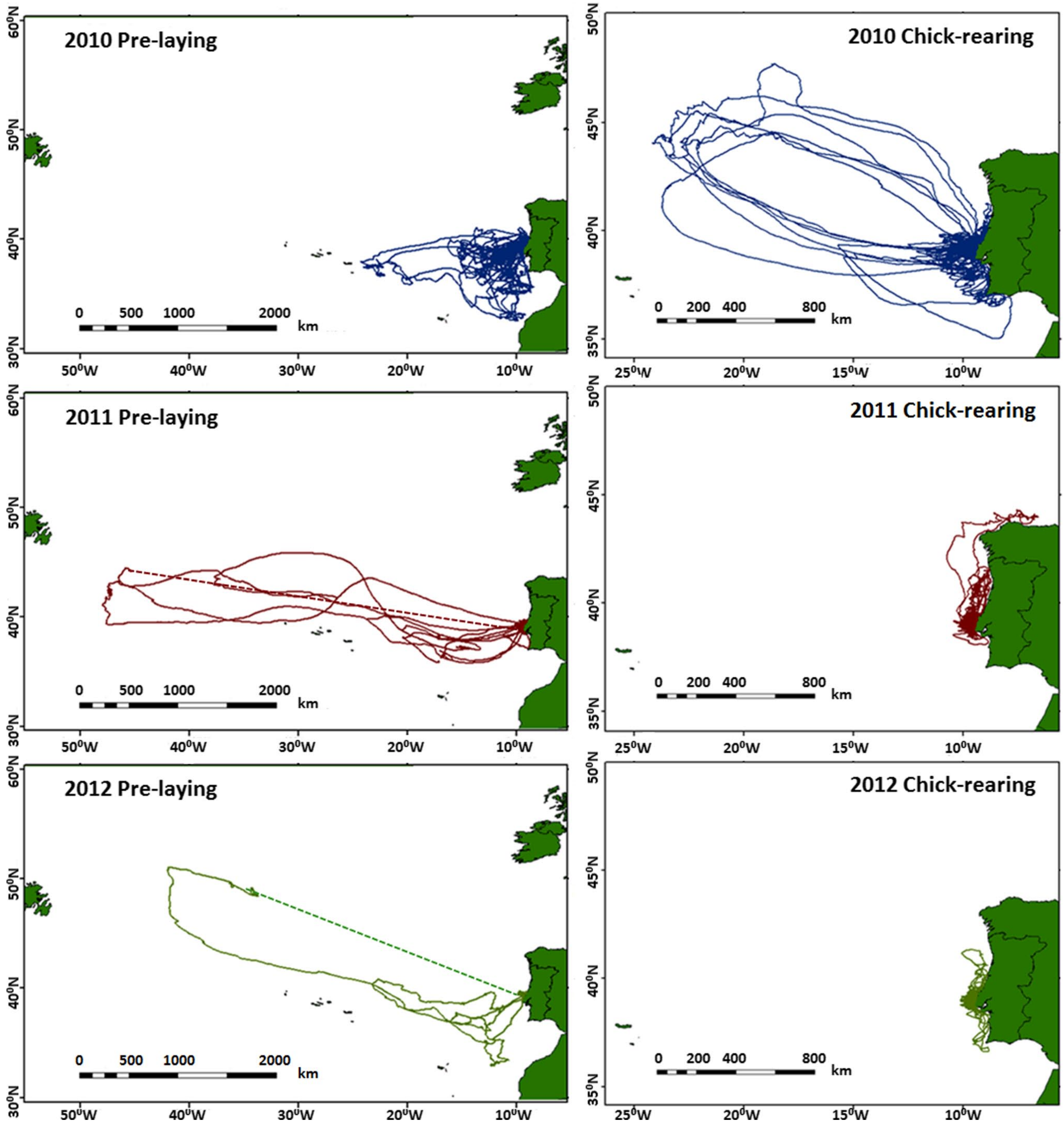

Fig. 1 GPS locations showing spatial distribution during foraging trips of Cory's shearwaters (*Calonectris diomedea*) breeding in Berlenga Island during the pre-laying and chick-rearing periods in 2010, 2011 and 2012 (pre-laying: n = 10, 8 and 12, respectively; chick-rearing: n = 19, 11 and 9, respectively). The *dashed lines* connecting the mid-Atlantic Ocean to Berlenga represent part of long foraging trips that were lost due to battery loss

δ^{13}C values during the chick-rearing period than during the pre-laying period (see Table 2 for multiple comparisons). However, we highlight that Cory's shearwaters exhibited substantial differences among all periods in the homogeneity of variances for both δ^{13}C and δ^{15}N of plasma (Levene's test: all $P < 0.001$), which provides a measure of trophic niche width (see Bearhop et al. 2004). A wide range of variances in both δ^{13}C and δ^{15}N of plasma and RBC suggest a variable isotopic niche width among periods. Specifically, SEAc index indicates a greater isotopic

Table 1 Comparison of means (Kruskal–Wallis test) and variances (Levene's test) of foraging parameters of Cory's shearwaters (*Calonectris diomedea*) breeding in Berlenga Island during the pre-laying (PL) and chick-rearing (CR) periods in 2010, 2011 and 2012

$h = 0.18°$	2010		2011		2012		Kruskal–Wallis test		Levene's test	
	PL ($n = 10$)	CR ($n = 19$)	PL ($n = 8$)	CR ($n = 11$)	PL ($n = 12$)	CR ($n = 9$)	$H_{(5,69)}$	P	$F_{(5,63)}$	P
Mean 25 % FKD (km^2)	2,189 ± 2,275	2,414 ± 1,450	2,424 ± 2,136	1,759 ± 716	1,914 ± 2,161	1,379 ± 685	7.4	0.19	3.6	**0.007**
Mean 50 % FKD (km^2)	6,331 ± 6,565	6,898 ± 4,536	11,062 ± 10,652	4,650 ± 1,905	6,031 ± 7,653	3,981 ± 2,877	9.7	0.08	5.4	**<0.001**
Mean 75 % FKD (km^2)	15,830 ± 16,722	15,724 ± 11331^{a}	39,882 ± 46963^{ab}	9,898 ± 4080^{b}	13,433 ± 18,554	8,708 ± 6,754	12.2	**0.033**	4.6	**0.001**
Mean max distance from colony (km)	341.4 ± 380.7^{a}	455.9 ± 478.8^{b}	1,510.2 ± 1,233.7^{abcd}	202.4 ± 136.0^{c}	423.2 ± 836.4	147.2 ± 86.2^{d}	16.0	**0.007**	10.2	**<0.001**
25 % FKD overlap (%)	4.5 ± 3.2^{a}	5.3 ± 2.3^{b}	3.2 ± 2.5^{c}	3.7 ± 2.2^{d}	3.7 ± 2.8^{e}	9.7 ± 3.3^{abcde}	18.8	**0.002**		
50 % FKD overlap (%)	13.3 ± 7.5^{a}	13.3 ± 3.7^{b}	9.8 ± 6.1^{c}	12.4 ± 5.8^{d}	11.7 ± 7.6^{e}	24.7 ± 4.8^{abcde}	22.2	**<0.001**		
75 % FKD overlap (%)	22.2 ± 11.5^{a}	22.2 ± 5.2^{bc}	15.5 ± 9.0^{bd}	26.2 ± 10.5^{e}	22.0 ± 13.3^{f}	41.8 ± 6.3^{acdef}	27.2	**<0.001**		
Latitude (° at max distance)	38.3 ± 1.5	40.0 ± 2.4	39.9 ± 2.3	40.3 ± 2.0	39.8 ± 4.0	38.3 ± 1.1	8.9	0.11		
Longitude (° at max distance)	−12.4 ± 4.6^{a}	−13.7 ± 5.9^{bc}	−26.8 ± 15.3^{abde}	−9.1 ± 0.6 ^{cd}	−13.6 ± 9.7	−9.4 ± 0.3^{e}	22.1	**<0.001**		

Values are mean ± SD. Significant results are in bold. Identical superscript letters indicate significant differences between periods (multiple comparisons)

Table 2 Stable isotope values of carbon (δ^{13}C) and nitrogen (δ^{15}N) and C/N mass ratio in plasma of Cory's shearwaters (*Calonectris diomedea*) breeding in Berlenga Island during the pre-laying (PL) and chick-rearing (CR) periods in 2010, 2011 and 2012

	2010		2011		2012		Kruskal–Wallis test		Levene's test	
	PL ($n = 10$)	CR ($n = 19$)	PL ($n = 8$)	CR ($n = 11$)	PL ($n = 12$)	CR ($n = 9$)	$H_{(5,69)}$	P	$F_{(5,63)}$	P
Plasma										
δ^{13}C (‰)	-19.5 ± 1.2^{abc}	-18.1 ± 0.6^{ad}	-18.9 ± 0.8	-18.2 ± 0.3^{be}	-19.2 ± 0.4^{de}	-18.4 ± 0.2^{c}	30.3	**<0.001**	13.3	**<0.001**
δ^{15}N (‰)	$+13.8 \pm 0.8$	$+13.4 \pm 0.6$	$+13.6 \pm 1.4$	$+14.3 \pm 0.4^{a}$	$+13.6 \pm 1.1$	$+12.8 \pm 0.2^{a}$	17.3	**0.004**	8.1	**<0.001**
C/N mass	4.28 ± 0.22	3.51 ± 0.10	3.50 ± 0.19	3.51 ± 0.08	4.12 ± 0.36	3.60 ± 0.09				
SEAc	1.37	0.85	2.34	0.26	1.50	0.12				
SEAb	2.49	1.24	3.21	0.95	2.08	0.90				
TA	1.95	2.25	3.44	0.41	2.57	0.20				
RBC										
δ^{13}C (‰)	-18.3 ± 0.7	-18.8 ± 0.5	-18.5 ± 0.6	-18.5 ± 0.2	-18.5 ± 0.4	-18.6 ± 0.2	5.7	0.34	5.3	**<0.001**
δ^{15}N (‰)	$+12.6 \pm 0.8$	$+12.8 \pm 0.5$	$+12.5 \pm 0.9^{a}$	$+13.5 \pm 0.2^{ab}$	$+13.0 \pm 0.8$	$+12.4 \pm 0.2^{b}$	20.5	**0.001**	4.1	**0.003**
SEAc	1.11	0.46	1.48	0.13	0.71	0.16				
SEAb	1.89	0.92	2.25	0.79	1.44	0.91				
TA	1.88	1.26	2.25	0.26	1.59	0.23				

The area of the standard ellipse (SEAc), the Bayesian approximation of the standard ellipse area (SEAb) 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 mean ± SD. Significant results are in bold. Identical superscript letters indicate significant differences between periods (multiple comparisons)

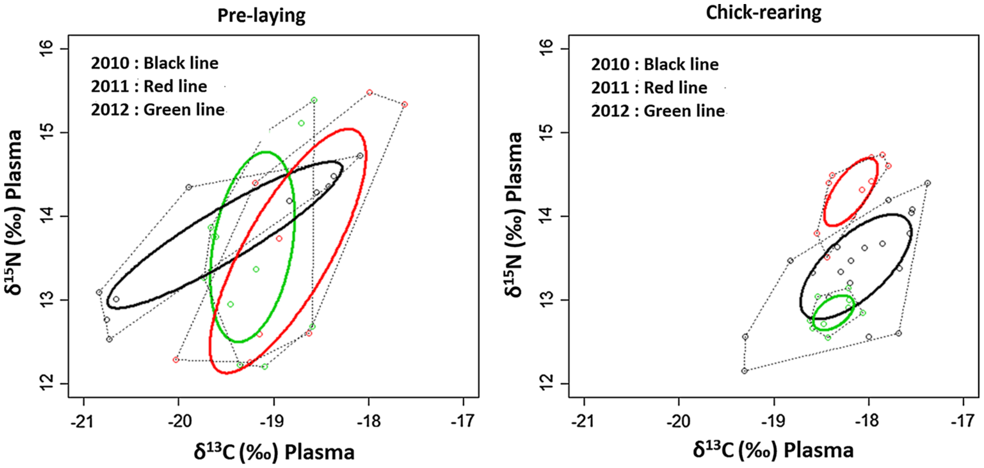

Fig. 2 Isotopic niche area based on stable isotope values (δ^{13}C and δ^{15}N) in plasma of Cory's shearwaters (*Calonectris diomedea*) breeding in Berlenga Island during the pre-laying and chick-rearing periods in 2010 (*black*), 2011(*red*) and 2012 (*green*). The area of the standard ellipses (SEAc, 40 % credible interval) was 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)

niche width during the 2011 pre-laying period and a lower isotopic niche width in the 2012 chick-rearing period (Fig. 2).

Overall, SIA results matched those of foraging parameters: Along the six studied periods, we found significant relationships between the isotopic niche width based on plasma and spatial distribution of birds; specifically, SEAc index was positive correlated with 50 % FKD area ($F_{1,4} = 16.7$, $P = 0.015$, $r^2 = 0.807$), 75 % FKD area ($F_{1,4} = 11.0$, $P = 0.029$, $r^2 = 0.734$) and maximum distance from colony ($F_{1,4} = 10.4$, $P = 0.032$, $r^2 = 0.723$). SEAb was positive correlated with 50 % FKD area ($F_{1,4} = 9.6$, $P = 0.036$, $r^2 = 0.707$) and 75 % FKD area ($F_{1,4} = 8.9$, $P = 0.040$, $r^2 = 0.690$). TA was positive correlated with 25 % FKD area ($F_{1,4} = 9.5$, $P = 0.037$, $r^2 = 0.705$) and 50 % FKD area ($F_{1,4} = 13.9$, $P = 0.020$, $r^2 = 0.777$).

Moreover, positive relationships were found between all isotopic niche width indices (SEAc, SEAb and TA) based on plasma, and the standard deviations of 25, 50, 75 % FKD and maximum distance from colony (all $P < 0.05$), with relevance to the relationship between SEAc and 50 % FKD standard deviation ($F_{1,4} = 144.7$, $P < 0.001$, $r^2 = 0.973$, Fig. 3), indicating a strong positive relationship between the variation in the area explored among individuals and isotopic niche width of the population. However, when split into both components of the isotopic niche (i.e. isotopic niche axis: trophic (δ^{15}N) and foraging habitat (δ^{13}C) components), these relationships were significant

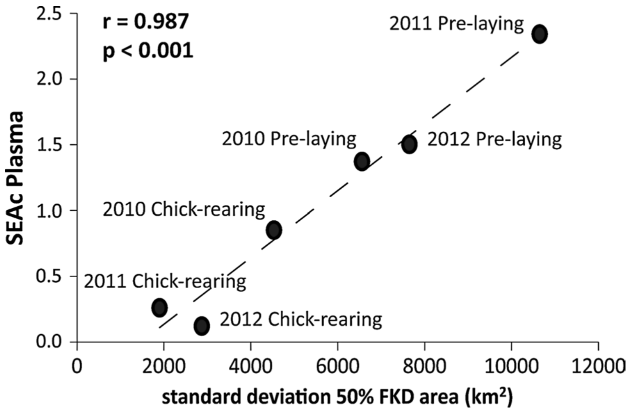

Fig. 3 Relationship between 50 % FKD (fixed kernel density, km^2) standard deviation and area of the standard ellipse (SEAc) based on plasma for the six sampling periods of Cory's shearwaters (*Calonectris diomedea*) breeding in Berlenga Island

with δ^{15}N standard deviation (all $P < 0.05$), but not with δ^{13}C standard deviation (all $P > 0.05$). This suggests that variations in the trophic level had a higher influence in driving the relationship between variation in the foraging range (GPS data) and isotopic niche width (SEAc, SEAb and TA), than variations in the foraging habitat.

Short-term consistency in the isotopic niche

Dissimilar patterns in short-term consistency in the isotopic niche of Cory's shearwaters were detected among years and between breeding periods. Positive significant relationships were found in δ^{15}N and in δ^{13}C between RBC and plasma of individual adults during both the pre-laying and chick-rearing periods (Fig. 4), suggesting short-term consistency during specific periods where relationships were detected. However, some differences were detected among the six sampling periods. Specifically, significant positive relationships were found in δ^{15}N and in δ^{13}C during the pre-laying period in 2010, 2011 and 2012, except for δ^{13}C in 2011. On the other hand, during the chick-rearing period, these relationships were not detected in 2012 for both δ^{15}N and δ^{13}C. Overall, these results suggest a main high short-term consistency in the isotopic niche within the population, but with exceptions such as those during the 2011 pre-laying and 2012 chick-rearing periods. Interestingly, the lack of consistency in these two periods matched the highest and lowest values of isotopic niche width, spatial distribution at sea and overlap in the estimated foraging range.

Breeding success and bird condition status

No significant differences were detected in body mass index and haematocrit values of Cory's shearwaters among the six periods (Table 3). However, laying success and breeding success of Cory's shearwaters on Berlenga differed significantly among years (Table 3); both were higher in 2012 than in the other 2 years.

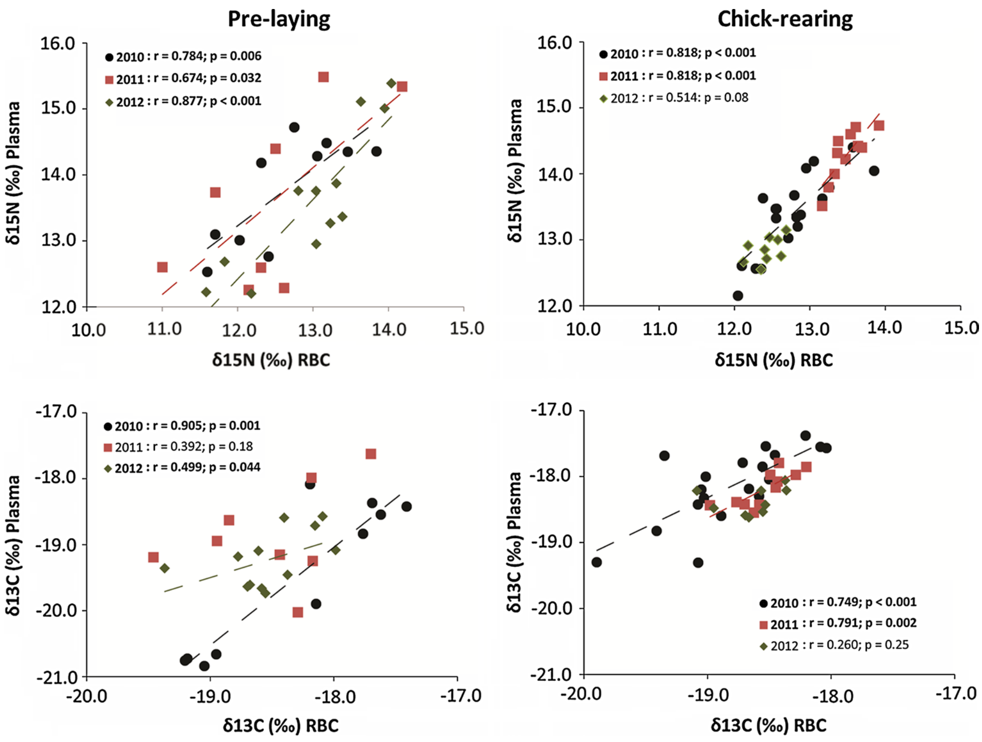

Fig. 4 Relationships in δ^{15}N (*upper panel*) and δ^{13}C (*lower panel*) between red blood cells (RBC) and plasma of Cory's shearwaters (*Calonectris diomedea*) breeding in Berlenga Island during the pre-laying (*left panel*) and chick-rearing (*right panel*) periods in 2010, 2011 and 2012

Table 3 Comparison of body mass index (BMI) and haematocrit of Cory's shearwaters (*Calonectris diomedea*) breeding in Berlenga Island during the pre-laying and chick-rearing periods in 2010, 2011 and 2012, and inter-annual comparison of laying success (number of eggs laid/number of nests) and breeding success (number of fledged birds/number of eggs laid)

	2010		2011		2012		Statistical comparison
	PL	CR	PL	CR	PL	CR	
BMI	−0.25 ± 1.03 (10)	−0.08 ± 1.12 (19)	0.36 ± 0.82 (8)	−0.61 ± 0.91 (11)	0.46 ± 0.45 (12)	0.26 ± 1.15 (9)	$F_{(5,63)} = 2.0; P = 0.10$
Haematocrit	0.45 ± 0.16 (10)	0.49 ± 0.11 (19)	0.49 ± 0.07 (8)	0.49 ± 0.05 (11)	0.50 ± 0.09 (12)	0.48 ± 0.04 (9)	$F_{(5,63)} = 0.3; P = 0.91$
Laying success (%)	47.7 (65)		49.2 (65)		80.0 (65)		$X^2_{(2)} = 17.9; P < 0.001$
Breeding success (%)	77.4 (31)		50.0 (32)		96.2 (52)		$X^2_{(2)} = 33.1; P < 0.001$

Values are mean ± SD (sample size)

Discussion

Cory's shearwater is dimorphic in size and bill dimensions (Granadeiro 1993, Ramos et al. 2009), suggesting possible at-sea foraging differences between sexes. Although the sex of sampled birds was identified in this study, the number of males sampled was much higher than the number of females, with the exception of 2010 (see "Materials and methods"). During some periods, only one female was sampled, and thus, we focused in the pooled data to test our hypothesis. However, we recognize that the degree of sexual differences can vary over time reflecting greater between-sex partitioning of resources when foraging ranges are more constrained and competition is greater (Phillips et al. 2011). Therefore, as we did not control for potential differences between males and females, our conclusions could be biased towards sex, although our focus was the inter-individual variability within the same population over the study period.

During the present study, Cory's shearwaters presented a great foraging plasticity between the pre-laying and chick-rearing periods, as expected and demonstrated before in other studies (Navarro et al. 2007; Paiva et al. 2010). However, the variability in foraging patterns also varied within periods and was greater in the 2011 pre-laying period and minor in the 2012 chick-rearing period. Interestingly, among other very long trips, we recorded an extraordinary trip that distanced 3,236 km from the colony in the 2011 pre-laying period (also see Paiva et al. 2013b). Such long trips are expected from populations breeding in oceanic islands (e.g. Magalhães et al. 2008 documented a mean maximum distance from the colony of 1,570 km during long trips of birds breeding in the eastern Azores, North Atlantic), but much less common for neritic areas such as Berlenga Island. The dramatic variation in the distribution and foraging behaviour of Cory's shearwaters during the 2011 pre-laying period (in relation to the other studied periods) should be attributed to a large-scale environmental variation determining a low abundance of pelagic fish prey along the Portuguese neritic system (Paiva et al. 2013a, b).

As expected, our results indicate generally positive significant relationships between the isotopic niche width (SEAc, SEAb and TA) and spatial distribution at sea (25, 50 and 75 % FKD area and maximum distance from colony) of Cory's shearwaters. Accordingly, when birds foraged farther from the colony, the isotopic niche also tended to expand. However, we highlight the strong relationships of variation in the foraging area among individuals with their isotopic niche width along the six periods, which are less influenced than previous parameters by sample size; low standard deviation values in the area explored (25, 50 and 75 % FKD and maximum distance from colony) were related with more even distribution of isotopic niches

(SEAc, SEAb and TA), which suggests that an increased variation in the spatial distribution at sea can lead to isotopic niche expansion of Cory's shearwaters. Although these results are in line with our predictions, our study considered similar isoscapes during the different periods and years throughout the foraging area used by Cory's shearwaters, limiting our conclusions regarding this issue. Therefore, it is not possible to know precisely, without analysis of base prey species over time and space, whether a wider isotopic niche during period "*x*" than during period "*y*" represents a wider dietary/trophic niche, or the same diet collected in areas or periods with different isotope baseline. However, it must be stressed that currently available isotopic landscapes in the NE Atlantic are fairly homogeneous, and seasonal changes in baseline δ^{15}N values for the North Atlantic are markedly lower than changes detected in our study (Montoya et al. 2002). Our results indicate that variations in the trophic level (i.e. in δ^{15}N), and not variations in the foraging habitat (i.e. in δ^{13}C), influenced significantly the observed relationship between variation in the foraging range and isotopic niche width. Although we cannot corroborate this hypothesis, this result suggests that isotopic niche expansion of the population might be attributed to greater diet diversity within the population, as a consequence of a higher variation in the area explored among individuals. These results are in line with community-wide metrics of trophic structure described by Layman et al. (2007) that relate wider trophic niche for a species to a greater amount of trophic diversity among individuals. Overall, as expected, our study suggests that a given population with more variability in spatial distribution at sea among its members shows wider isotopic niche than the same population with less variability in foraging areas among individuals. The reasons for this are not clear but our data suggest that changes in trophic position, arising for example from dietary changes, are the most likely causes.

Niche variation among individuals may have several implications affecting whole population dynamics (Bolnick et al. 2011), including the individual specialization in the specific resources used (Svanbäck and Bolnick 2007; this study). Our results documented short-term consistency (within about 1 month) in the isotopic niche of Cory's shearwaters in four out of six periods, which highlights individual preferences among birds during these periods, as demonstrated in other species such as albatrosses (Weimerskirch et al. 2005), guillemots (Woo et al. 2008), gannets (Votier et al. 2010), skuas (Votier et al. 2004) and gulls (Ceia et al. 2014). Interestingly, in two periods, the short-term consistency in the isotopic niche of Cory's shearwaters was not verified. Specifically, during the 2011 pre-laying period, no relationship was detected in δ^{13}C between RBC and plasma of individual adults, and during the 2012 chick-rearing period, no relationships were detected either in δ^{15}N and δ^{13}C. Bolnick et al. (2010) found that individual and population niche widths are decoupled; in fact, our results suggested a lack of short-term consistency (i.e. the variation within individuals was greater than variation among individuals) when population isotopic niche width was highest (2011 pre-laying period) and smallest (2012 chick-rearing period), indicating that individual consistency in resources use of Cory's shearwaters may fluctuate over time (i.e. among years and periods). In the 2011 pre-laying period, birds performed very long trips and did not show short-term consistency in carbon source, most probably because previous trips were presumably not in the same area due to anomalies at very large scales (Weimerskirch 2007), which mainly influences the geographic distribution of δ^{13}C in marine pelagic systems (Cherel and Hobson 2007). On the other hand, in the 2012 chick-rearing period, birds performed shorter trips with high overlap in foraging areas among birds, resulting in less variance among individuals. Because they probably preyed on the same few but presumably superabundant resources during the 2012 chick-rearing period, the population isotopic niche width tended to be narrower than if they preyed on a broad spectrum of items (Bearhop et al. 2004).

Fluctuations on consistency may be related to temporal changes in the availability and predictability of resources (Svanbäck and Persson 2004; Woo et al. 2008). Although we have no data on prey availability and distribution, our results suggested a role for differences in the availability of resources because birds varied their individual foraging strategies among years and periods leading to fluctuations in short-term consistency, particularly during the 2011 pre-laying and the 2012 chick-rearing periods. Moreover, our data showed a small breeding participation in 2011, in opposition to 2012, suggesting contrasting breeding conditions that could be derived by food availability. We found no evidence that condition status of birds was affected among years and periods; however, it is believed that shearwaters present a fixed investment, which means that they increase the foraging effort to maintain their body condition and reduce parental investment, with a consequent reduction in breeding success (Navarro and González-Solís 2007). Apparently, birds preferred to forage farther in the 2011 pre-laying period because of lack of resources around the colony in contrast with the 2012 chick-rearing period, when birds preferred to forage in adjacent areas to the colony. A lower abundance of foods might favour niche width expansion of a single population via greater between-individual variation, because some individuals can shift their diet pursuing different resources (Svanbäck and Bolnick 2007; Bolnick et al. 2010; Ceia et al. 2014). Our results matched with this hypothesis because the Cory's shearwater isotopic niche width was smaller in the 2012 chick-rearing period (corroborated with a higher overlap in the foraging area) possibly attributed to high abundance of food resources, in contrast with the 2011 pre-laying period. During all other periods, short-term consistency in the isotopic niche (i.e. greater variation among individuals than within individuals) of Cory's shearwaters was relatively high and persistent. In this case, birds may have a narrow foraging niche (i.e. individuals use a subset of their population's niche) presumably helping to reduce intra-specific competition as demonstrated in other seabird species such as northern gannets *Morus bassanus* (Votier et al. 2010) and wandering albatrosses *Diomedea exulans* (Ceia et al. 2012).

In summary, our results confirm a strong positive relationship between spatial distribution at sea and isotopic niche width of a pelagic seabird population. This relationship is particularly relevant considering variation among individuals in spatial distribution at sea, i.e. low standard deviations values correspond to a more even distribution of isotopic niches and vice versa. Cory's shearwaters showed high short-term consistency in the isotopic niche (within about 1 month) in four out of six periods during this study (during both pre-laying and chick-rearing periods). We documented fluctuations on short-term consistency in the isotopic niche of Cory's shearwaters related to their markedly different foraging patterns (i.e. in spatial distribution at sea and isotopic niche width) in the 2011 pre-laying and 2012 chick-rearing periods. The short-term consistency in the isotopic niche was not verified in circumstances of very small variation in the spatial distributions at sea and small isotopic niche width. Interestingly, consistency was also not verified in the opposite extreme patterns documented during this study. Thus, consistency in isotopic niche (i.e. individual preferences) appears to be an individual's trait that should drive the dynamics of Cory's shearwater foraging ecology, and possibly related pelagic species; the fluctuations of such trait could be related to temporal changes in the availability and predictability of resources, and its advantages may relate with an attempt to reduce intra-specific competition among individuals, but further studies must be conducted to validate this hypothesis.

Acknowledgments This research was cosponsored by the Foundation for Science and Technology (Portugal) and the European Social Found (POPH, EU) through a PhD grant attributed to Filipe R. Ceia (SFRH/BD/64558/2009) and a postdoc grant attributed to Vitor H. Paiva (SFRH/BDP/63825/2009), and by the project FAME (Future of the Atlantic Marine Environment; Project No. 2009-1/089—Atlantic Area) funded by the EU. We are grateful to the support given by the Berlengas Nature Reserve for permission to work on the island and for providing accommodation. Special thanks to wardens P. Crisóstomo and E. Mourato. We thank A. Werner, F. Haug, V. Fidalgo and M. Soares for help in the field and C. Docal and A. Baeta for running stable isotope samples.

References

Bearhop S, Teece MA, Waldron S, Furness RW (2000) Influence of lipid and uric acid on δ13C and δ15 N values of avian blood: implications for trophic studies. Auk 117:504–507

Bearhop S, Adams CE, Waldron S, Fuller RA, Macleod H (2004) Determining trophic niche width: a novel approach using stable isotope analysis. J Anim Ecol 73:1007–1012

Bearhop S, Phillips RA, McGill R, Cherel Y, Dawson DA, Croxall JP (2006) Stable isotopes indicate sex-specific and long-term individual foraging specialisation in diving seabirds. Mar Ecol Prog Ser 311:157–164

Bolnick DI, Svanbäck R, Fordyce JA, Yang LH, Davis JM, Hulsey CD, Forister ML (2003) The ecology of individuals: incidence and implications of individual specialization. Am Nat 161:1–28

Bolnick DI, Svanbäck R, Araújo MS, Persson L (2007) Comparative support for the niche variation hypothesis that more generalized populations also are more heterogeneous. Proc Natl Acad Sci USA 104:10075–10079

Bolnick DI, Ingram T, Stutz WE, Snowberg LK, Lau OL, Paull JS (2010) Ecological release from interspecific competition leads to decoupled changes in population and individual niche width. Proc R Soc B 277:1789–1797

Bolnick DI, Amarasekare P, Araújo MS, Bürger R, Levine JM, Novak M, Rudolf VHW, Schreiber SJ, Urban MC, Vasseur DA (2011) Why intraspecific trait variation matters in community ecology. Trends Ecol Evol 26:183–192

Calenge C (2006) The package "adehabitat" for the R software: a tool for the analysis of space and habitat use by animals. Ecol Modell 197:516–519

Ceia FR, Phillips RA, Ramos JA, Cherel Y, Vieira RP, Richard P, Xavier JC (2012) Short- and long-term consistency in the foraging niche of wandering albatrosses. Mar Biol 159:1581–1591

Ceia FR, Paiva VH, Fidalgo V, Morais L, Baeta A, Crisóstomo P, Mourato E, Garthe S, Marques JC, Ramos JA (2014) Annual and seasonal consistency in the feeding ecology of an opportunistic species, the yellow-legged gull *Larus michahellis*. Mar Ecol Prog Ser 497:273–284

Cherel Y, Hobson KA (2007) Geographical variation in carbon stable isotope signatures of marine predators: a tool to investigate their foraging areas in the Southern Ocean. Mar Ecol Prog Ser 329:281–287

Cherel Y, Hobson KA, Hassani S (2005a) Isotopic discrimination between food and blood and feathers of captive penguins: implications for dietary studies in the wild. Physiol Biochem Zool 78:106–115

Cherel Y, Hobson KA, Weimerskirch H (2005b) Using stable isotopes to study resource acquisition and allocation in procellariiform seabirds. Oecologia 145:533–540

Fair J, Whitaker S, Pearson B (2007) Sources of variation in haematocrit in birds. Ibis 149:535–552

Fieberg J, Kochanny CO (2005) Quantifying home-range overlap: the importance of the utilization distribution. J Wildl Manag 69:1346–1359

Granadeiro JP (1993) Variation in measurements of Cory's shearwater between populations and sexing by discriminant analysis. Ring Migr 14:103–112

Igual JM, Forero MG, Tavecchia G, González-Solis J, Martínez-Abraín A, Hobson KA, Ruiz X, Oro D (2005) Short-term effects of data-loggers on Cory's shearwater (*Calonectris diomedea*). Mar Biol 146:619–624

Jackson AL, Inger R, Parnell AC, Bearhop S (2011) Comparing isotopic niche widths among and within communities: SIBER—stable isotope bayesian ellipses in R. J Anim Ecol 80:595–602

Jaeger A, Lecomte VJ, Weimerskirch H, Richard P, Cherel Y (2010) Seabird satellite tracking validates the use of latitudinal isoscapes to depict predators' foraging areas in the Southern Ocean. Rapid Commun Mass Spectrom 24:3456–3460

Layman CA, Arrington DA, Montaña CG, Post DM (2007) Can stable isotope ratios provide for community-wide measures of trophic structure? Ecology 88:42–48

Lecoq M, Geraldes P, Andrade J (2011) First complete census of Cory's Shearwaters *Calonectris diomedea borealis* breeding at Berlengas Islands (Portugal), including the small islets of the archipelago. Airo 21:31–34

Louzao M, Bécares J, Rodríguez B, Hyrenbach K, Ruiz A, Arcos J (2009) Combining vessel-based surveys and tracking data to identify key marine areas for seabirds. Mar Ecol Prog Ser 391:183–197

Magalhães M, Santos R, Hamer K (2008) Dual-foraging of Cory's shearwaters in the Azores: feeding locations, behaviour at sea and implications for food provisioning of chicks. Mar Ecol Prog Ser 359:283–293

Matich P, Heithaus MR, Layman CA (2011) Contrasting patterns of individual specialization and trophic coupling in two marine apex predators. J Anim Ecol 80:294–305

Montoya J, Carpenter E, Capone D (2002) Nitrogen fixation and nitrogen isotope abundances in zooplankton of the oligotrophic North Atlantic. Limnol Oceanogr 47:1617–1628

Nakagawa S, Schielzeth H (2010) Repeatability for Gaussian and non-Gaussian data: a practical guide for biologists. Biol Rev Camb Philos Soc 85:935–956

Navarro J, González-Solís J (2007) Experimental increase of flying costs in a pelagic seabird: effects on foraging strategies, nutritional state and chick condition. Oecologia 151:150–160

Navarro J, González-Solís J, Viscor G (2007) Nutritional and feeding ecology in Cory's shearwater *Calonectris diomedea* during breeding. Mar Ecol Prog Ser 351:261–271

Neves V, Nolf D, Clarke M (2012) Spatio-temporal variation in the diet of Cory's shearwater *Calonectris diomedea* in the Azores archipelago, northeast Atlantic. Deep Sea Res Part I 70:1–13

Newsome SD, del Rio CM, Bearhop S, Phillips DL (2007) A niche for isotopic ecology. Front Ecol Environ 5:429–436

Paiva VH, Geraldes P, Ramírez I, Meirinho A, Garthe S, Ramos JA (2010) Foraging plasticity in a pelagic seabird species along a marine productivity gradient. Mar Ecol Prog Ser 398:259–274

Paiva VH, Geraldes P, Marques V, Rodríguez R, Garthe S, Ramos JA (2013a) Effects of environmental variability on different trophic levels of the North Atlantic food web. Mar Ecol Prog Ser 477:15–28

Paiva VH, Geraldes P, Ramirez I, Werner A, Garthe S, Ramos JA (2013b) Overcoming difficult times: the behavioural resilience of a marine predator when facing environmental stochasticity. Mar Ecol Prog Ser 486:277–288

Parnell AC, Inger R, Bearhop S, Jackson AL (2010) Source partitioning using stable isotopes: coping with too much variation. PLoS ONE 5:e9672

Phillips RA, Xavier JC, Croxall JP (2003) Effects of satellite transmitters on albatrosses and petrels. Auk 120:1082–1090

Phillips RA, Bearhop S, McGill RAR, Dawson DA (2009) Stable isotopes reveal individual variation in migration strategies and habitat preferences in a suite of seabirds during the nonbreeding period. Oecologia 160:795–806

Phillips RA, McGill RAR, Dawson DA, Bearhop S (2011) Sexual segregation in distribution, diet and trophic level of seabirds: insights from stable isotope analysis. Mar Biol 158:2199–2208

Ramos JA, Granadeiro JP, Phillips RA, Catry P (2009) Flight morphology and foraging behavior of male and female Cory's shearwaters. Condor 111:424–432

Sánchez-Guzmán JM, Villegas A, Corbacho C, Morán R, Marzal A, Real R (2004) Response of the haematocrit to body condition changes in Northern Bald Ibis *Geronticus eremita*. Comp Biochem Physiol Part A 139:41–47

Soanes LM, Arnould JPY, Dodd SG, Sumner MD, Green JA (2013) How many seabirds do we need to track to define home-range area? J Appl Ecol 50:671–679

Sousa FM, Nascimento S, Casimiro H, Boutov D (2008) Identification of upwelling areas on sea surface temperature images using fuzzy clustering. Remote Sens Environ 112:2817–2823

Svanbäck R, Bolnick DI (2007) Intraspecific competition drives increased resource use diversity within a natural population. Proc R Soc B 274:839–844

Svanbäck R, Persson L (2004) Individual diet specialization, niche width and population dynamics: implications for trophic polymorphisms. J Anim Ecol 73:973–982

Syvaranta J, Lensu A, Marjomaki TJ, Oksanen S, Jones RI (2013) An empirical evaluation of the utility of convex hull and standard ellipse areas for assessing population niche widths from stable isotope data. PLoS ONE 8:e56094

Tinker MT, Bentall G, Estes JA (2008) Food limitation leads to behavioral diversification and dietary specialization in sea otters. Proc Natl Acad Sci USA 105:560–565

Van Valen L (1965) Morphological variation and width of ecological niche. Am Nat 99:377–389

Vandenabeele SP, Shepard EL, Grogan A, Wilson RP (2012) When three per cent may not be three per cent; device-equipped seabirds experience variable flight constraints. Mar Biol 159:1–14

Votier SC, Bearhop S, Ratcliffe N, Furness RW (2004) Reproductive consequences for great skuas specializing as seabird predators. Condor 106:275–287

Votier SC, Bearhop S, Witt MJ, Inger R, Thompson D, Newton J (2010) Individual responses of seabirds to commercial fisheries revealed using GPS tracking, stable isotopes and vessel monitoring systems. J Appl Ecol 47:487–497

Weimerskirch H (2007) Are seabirds foraging for unpredictable resources? Deep Sea Res Part II 54:211–223

Weimerskirch H, Bonadonna F, Bailleul F, Mabille G, Dell'Omo G, Lipp H-P (2002) GPS tracking of foraging albatrosses. Science 295:1259

Weimerskirch H, Gault A, Cherel Y (2005) Prey distribution and patchiness: factors in foraging success and efficiency of wandering albatrosses. Ecology 86:2611–2622

Woo KJ, Elliott KH, Davidson M, Gaston AJ, Davoren GK (2008) Individual specialization in diet by a generalist marine predator reflects specialization in foraging behaviour. J Anim Ecol 77:1082–1091

Xavier JC, Magalhães MC, Mendonça AS, Antunes M, Carvalho N, Machete M, Santos RS, Paiva V, Hamer KC (2011) Changes in diet of Cory's Shearwaters *Calonectris diomedea* breeding in the Azores. Mar Ornithol 39:129–134