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Seasonally persistent foraging niche segregation between sympatric Southern Rockhopper and Magellanic penguins breeding at Isla de los Estados, Argentina

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Abstract

Variation in the foraging strategies used among species is a key factor in determining the trophic structure of ecological communities. Moreover, foraging niche differentiation could be driven by inter-specific competition and/or variation within species due to seasonal, age, sex and/or individual factors. Using stable isotope analysis, we assessed inter- and intra-specific differences in the foraging niches of female Southern Rockhopper penguin (*Eudyptes chrysocome*; SRP) and male and female Magellanic penguins (*Spheniscus magellanicus*; MP) at Isla de los Estados, Argentina. We sampled whole blood and feathers from breeding adults, representing the breeding and pre-moult periods over two consecutive years (2012 and 2013). We also compared stable isotope values between tissue to test for consistency in individuals foraging niches and the potential for foraging niche specialisation and segregation within breeding pairs. We observed clear foraging niche segregation between species that persisted during both breeding and pre-moult periods. SRP foraged in more oceanic/pelagic waters (lower $\delta^{13}\text{C}$ values) while MP used coastal/benthic foraging habitats (higher $\delta^{13}\text{C}$ values). In addition, SRP fed on lower trophic level prey (low $\delta^{15}\text{N}$ values) relative to MP during both time periods. The isotopic foraging niches of MP highly overlapped between sexes at the population level and there was little to no evidence of niche segregation within breeding pairs or individual consistency in the seasonal foraging niche of both species. The results suggest that inter-specific foraging niche segregation is likely a more important factor influencing the trophic ecology and foraging behaviours of these species, relative to intra-specific factors. Even so, the persistence of inter-specific foraging niche segregation outside the breeding season suggests that either the potential for competition for food resource or foraging habitats remain high during this time or that the ultimate factors responsible for foraging niche segregation among these two species may be unrelated to these proximate factors.

Keywords *Spheniscus magellanicus* · *Eudyptes chrysocome* · Inter-specific competition · Intra-specific competition · Individual consistency

Zusammenfassung

Saisonal anhaltende Nischensegregation zwischen sympatrischen Felsenpinguin und Magellan-Pinguinen, die auf der Isla de los Estados in Argentinien brüten

Variabilität in den Futersuchstrategien zwischen Arten ist ein Schlüsselfaktor für die Bestimmung der trophischen Struktur ökologischer Gemeinschaften. Differenzierung in der Nahrungssuche könnte zusätzlich durch interspezifische Konkurrenz und/oder innerartliche Variation aufgrund saisonaler, altersbedingter, geschlechtsspezifischer und/oder individueller Faktoren bestimmt sein. Durch die Analyse von stabilen Isotopen untersuchten wir inter- und intraspezifische Unterschiede in der

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Nahrungssuche von weiblichen Felsenpinguinen (*Eudyptes chrysolophus*; SRP) und männlichen und weiblichen Magellan-Pinguinen (*Spheniscus magellanicus*; MP) auf der Isla de los Estados in Argentinien. In zwei aufeinander folgenden Jahren (2012 und 2013) haben wir sowohl zur Brutzeit wie zur Mauserzeit Blut und Federn von brütenden Altvögeln gesammelt. Auch haben wir Stabile Isotopen zwischen Geweben verglichen, um die Konsistenz der individuellen Nahrungsnische sowie das Potenzial für die Spezialisierung und Segregation von Nahrungsnischen innerhalb von Brutpaaren zu testen. Wir beobachteten eine klare Segregation der Nahrungsnischen zwischen den Arten, die während der Brut- und der Mauserzeit fortbestanden. SRP suchten nach Futter vornehmlich in ozeanischen/pelagischen Gewässern (niedrigere $\delta^{13}\text{C}$ -Werte), MP dagegen in küstennahen/benthischen Nahrungslebensräumen (höhere $\delta^{13}\text{C}$ -Werte). Außerdem ernährten sich SRP während beider Zeiträume von Beute mit niedrigerem trophischen Niveau (niedrige $\delta^{15}\text{N}$ -Werte). Die über die Isotopenzusammensetzung ermittelten Nahrungsnischen von MP überlagerten sich auf Populationsebene stark zwischen Geschlechtern, doch es fanden sich keine deutlichen Hinweise auf eine Nischentrennung innerhalb der Brutpaare oder auf individuelle Konsistenz in der saisonalen Nahrungsnische beider Arten. Die Ergebnisse deuten darauf hin, dass die interspezifische Nischensegregation bei der Nahrungssuche wahrscheinlich ein wichtigerer Faktor ist, im Vergleich zu intra-spezifischen Faktoren, die die trophische Ökologie und das Nahrungssuchverhalten dieser Arten beeinflusst. Das Fortbestehen einer interspezifischen Nischensegregation außerhalb der Brutzeit lässt darauf schließen, dass entweder das Konkurrenzpotenzial um Nahrungsressourcen oder Nahrungslebensräume während dieser Zeit hoch bleibt, oder dass die ultimativen Faktoren, die für die Segregation der Nahrungsnischen der beiden Arten unabhängig von diesen proximalen Faktoren sind.

Introduction

Inter- and intra-specific variation in the foraging strategies of species are important determinants of the overall trophic structure of communities (Begon et al. 2006). Moreover, species' niches may also vary in relation to the stage of the annual cycle, age, sex and/or individual preferences on prey type and foraging areas (Bolnick et al. 2003). This broadens the population niche and allows different mechanisms by which inter- and intra-specific competition can be reduced (Bolnick et al. 2003).

Niche segregation in seabirds is commonly studied during the breeding season when individuals are central place foragers, thus constrained to only exploit resources within a foraging range around their colonies and/or nesting area (Costa 1991; Grémillet et al. 2004). Therefore some inter- and intra-specific partitioning is usually expected in the use of available food resources, according to the principle of competitive exclusion (Hutchinson 1957; Lewis et al. 2001; Rosciano et al. 2016), since they forage in environments with temporally and/or spatially limited resources.

However, once the breeding season is over, and chicks fledge, adults are no longer restricted in time and/or space to forage to bring back the food on time to their chicks (e.g. Boersma and Rebstock 2009). During this time period, penguins leave the colonies for approximately two weeks to replenish and store energy reserves before they start to moult, usually at the same colony where they breed (Boersma et al. 2013; Trathan et al. 2014). Although this intensive feeding could potentially generate competition, the ability to explore and use larger/more distant foraging areas may also reduce competitive overlap and relax foraging niche segregation between and within species

(Dehnhard et al. 2011; Thiebot et al. 2014; Silva et al. 2014).

Sexual segregation and individual consistency are additional factors that may act to reduce intra-specific competition within populations. Sexual segregation in foraging strategies is usually more intense during the reproductive period (incubation and/or chick rearing) and is commonly associated with the degree of dimorphism that a species presents (e.g. Forero et al. 2005; Raya Rey et al. 2012; Ludynia et al. 2013). However, little is known about whether there is niche specialisation at the couple level (e.g. Phillips et al. 2005; Phillips et al. 2011). Moreover, individuals can use a limited fraction of a range of resources used by the population, generating large inter-individual niche variation that can be constant along short and/or long periods of time (Bolnick et al. 2003). For instance, a previous study of female Southern Rockhopper penguins reported individually consistent foraging niches between years during the pre-breeding period (Dehnhard et al. 2016).

Stable isotope analysis is commonly used to define the trophic niche of consumers (Newsome et al. 2007). For instance, nitrogen stable isotope values ($\delta^{15}\text{N}$) reflect the trophic position of consumers due to a stepwise enrichment of ^{15}N between trophic levels (Minagawa and Wada 1984; Post 2002). Carbon stable isotope values ($\delta^{13}\text{C}$) reflect the foraging habitat of seabirds and other marine consumers as inshore/benthic foraging habitats have higher $\delta^{13}\text{C}$ values relative to offshore/pelagic habitats (Hobson et al. 1997; France 1995; Cherel and Hobson 2007). Moreover, tissues integrate stable isotope values at differing temporal scales (e.g. Ceia et al. 2012; Herman et al. 2017). For example, penguin feathers reflect diet previous to moult since keratin

is metabolically inert after synthesis (Mizutani et al. 1991; Cherel et al. 2000; Bearhop et al. 2002) and whole blood gives information on the diet consumed within a range of 2–4 weeks (Barquete et al. 2013). Therefore, when comparing isotope values of different tissues coming from the same individual provides information on short/long-term consistency of the isotopic niche (Ceia et al. 2012, 2014) and allows examination of variation at the level of an individual and/or population through time.

In this study, our objective was to assess inter- and intra-specific foraging niche segregation between sympatric penguin species on Isla de los Estados during the breeding and post-breeding, pre-moult periods. Using the isotopic niche approach, we compared the foraging niches of female Southern Rockhopper penguin (*Eudyptes chrysocome*; hereafter “Rockhopper penguin”) and male and female Magellanic penguins (*Spheniscus magellanicus*) using whole blood (breeding) and feather (pre-moult) samples. We hypothesised that both inter- and intra-specific niche segregation would be stronger during the breeding season due to the higher potential for competition for food resources experienced as central place foragers, while raising chicks (e.g. Rosciano et al. 2016), relative to the post-breeding period when adults are less restricted in their foraging range and trip duration. Individual foraging specialisation within a population may be highly time dependent and thus it is recommended to sample across different time periods within years to assess individual consistency (e.g. Dehnhard et al. 2016). Thus, we compared the stable isotope values of tissue reflecting differing time periods (i.e. breeding and pre-moult periods) to test for seasonal consistency in individual foraging niches and the potential for individual foraging niche specialisation.

Methods

Study site, sample collection and preparation

We conducted field work from late November to mid-December, during the early chick rearing period of the breeding season of two consecutive years (2012 and 2013) at Isla de los Estados, Tierra del Fuego, Argentina ($54^{\circ} 55' S$ – $64^{\circ} 46' W$, Fig. 1). We collected samples from breeding adult Magellanic and Rockhopper penguins that were found attending active nests. For Magellanic penguins, we sampled both individuals (i.e. a pair) attending the nest, as males and females share the parental duties during the early chick rearing period (Boersma et al. 1990, 2013). We sampled only adult female Southern Rockhopper penguins since they feed their chicks during the early chick rearing period, while males remain at the nest guarding (Warham 1975; Pütz et al. 2013).

When sampling adults of both species, we gently removed them from their nests, weighed them using a Pesola spring balance (to the nearest 100 g) and measured their bill depth and bill length using callipers (to the nearest 0.1 mm) to determine sex (Gandini et al. 1992; Hull 1996). From each individual, we collected whole blood in microcapillary tubes (approximately 75 μ l from the tarsal vein) and feathers (5–8 randomly selected from the penguins back). We preserved the blood samples in 70% ethanol and feathers in plastic bags until subsequent processing in the laboratory. Several studies in the past showed little effect of alcohol preservation on the stable isotope values of blood (Hobson et al. 1997; Halley et al. 2008; Therrien and Fitzgerald 2011). Whole blood samples in this study represent the dietary history of the adults primarily during early chick rearing, but may also include a portion of the late incubation

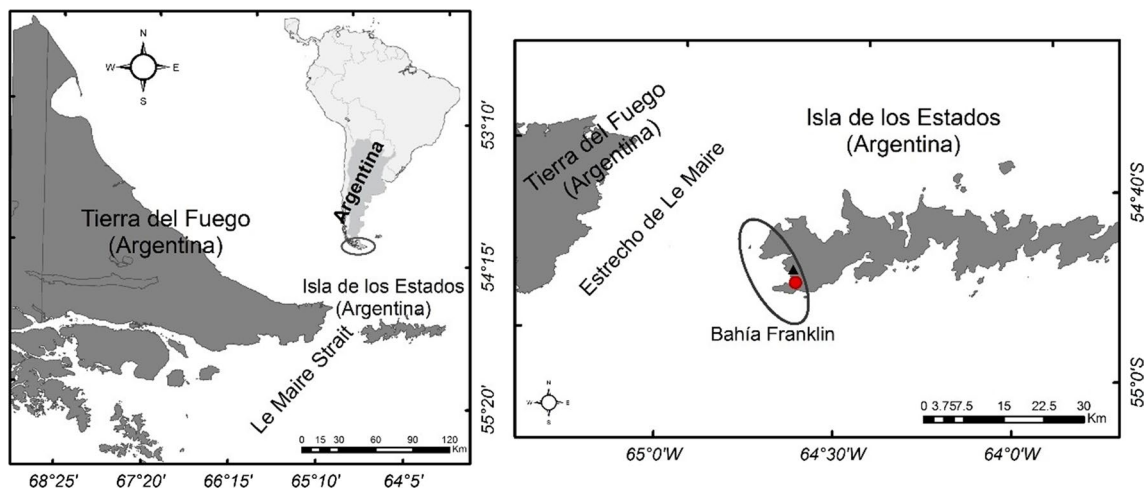


Fig. 1 The study area is located in Tierra del Fuego province, Argentina. The Rockhopper penguin colony sampled is marked with a triangle and the Magellanic penguin colony location with a circle

period as well for both species of penguins, as the turnover rate for this tissue is between 20 and 30 days (Bearhop et al. 2002; Barquete et al. 2013). Feathers are representative of the pre-moult foraging period, as the moult occurs a few weeks after the breeding season and feathers are metabolically inert after synthesis (Mizutani et al. 1991; Cherel et al. 2000; Bearhop et al. 2002).

Feather samples were cleaned using 2:1 chloroform:methanol rinse, air-dried and later cut into small fragments with stainless steel scissors. Whole blood samples were dried in an oven at 60 °C and then freeze-dried for 24 h in a lyophiliser. We then weighed out approximately 0.5 mg of each type of sample (feather and whole blood) into tin cups that were flash-combusted (Costech ECS4010 elemental analysers) to analyse for carbon and nitrogen isotopes ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) through an interfaced continuous-flow stable isotope ratio mass spectrometer (Thermo Scientific Delta V Plus). Sample precision based on the repeated sample and reference material was 0.2‰ for $\delta^{13}\text{C}$ and 0.3‰ for $\delta^{15}\text{N}$. Stable isotope abundances are expressed in δ notation in per mille units (‰), according to the following equation:

$$\delta X = \left(\frac{R_{\text{sample}}}{R_{\text{standard}}} - 1 \right) \times 1000,$$

where X is ^{13}C or ^{15}N and R is the corresponding ratio $^{13}\text{C}:^{12}\text{C}$ or $^{15}\text{N}:^{14}\text{N}$. The R_{standard} values were based on the Vienna PeeDee Belemnite (VPDB) for ^{13}C and atmospheric N_2 for ^{15}N . Whole blood $\delta^{13}\text{C}$ values were normalized for the effects of lipid concentration on $\delta^{13}\text{C}$ methods following Post et al. (2007) as C:N ratio values indicated variable concentration of ^{13}C -depleted lipids, similar to other penguin species (Cherel et al. 2005b; Hedd and Montevecchi 2006).

Statistical analysis

To compare foraging niche position and overlap between penguin groups (species/sex) for the breeding and pre-moult periods (post-breeding) of the two years sampled separately, we calculated the Euclidean distance between group centroids (following methods in Turner et al. 2010). If significant differences between niche positions (ED) were identified using this multivariate approach, we then used t tests for independent samples (for normally distributed data) or Wilcoxon tests (for non-normally distributed data) to detect which isotopic niche axis ($\delta^{13}\text{C}$ and/or $\delta^{15}\text{N}$) contributed to the observed differences (Hammer-schlag-Peyer et al. 2011).

To compare niche area and overlap among penguin groups (species/sex) during the breeding and pre-moult (whole blood and feathers separately) periods in each year, we used standard ellipse areas (SEA_C , corrected for small sample size; Jackson et al. 2011) and the Bayesian

approximation with corresponding 95% confidence intervals (SEA_b ; Jackson et al. 2011) to quantify the uncertainty of the core isotopic niche areas. Finally, we calculated total isotopic niche area (TA) as the area of the smallest convex hull that contains all individuals of a group in a $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ bi-plot (Layman et al. 2007). TA can be interpreted as a measure of the total foraging niche width of a population, as it does not exclude individual niches from the characterisation of the population niche (Layman and Allgeier 2012).

To account for individual consistency and specialisation in foraging habitat and trophic level, we performed regression analysis (linear mixed effect models, LMM) between $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotope values of blood vs feathers for each species/sex group (female rockhopper penguins and male and female Magellanic penguin), using year (2012 and 2013) as a random factor to account for inter-annual variation.

To study niche segregation between and within couples of Magellanic penguins, we performed LMM for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of each tissue (blood and feathers) separately. We used sex as explanatory variable if it improved the fit of the model and we fitted a variance structure if the homogeneity of variance assumption was not met (VarIdent function; Zuur et al. 2009). We used nest ID nested in year as the random factor of the model and performed variance components analysis to calculate the proportion of the variance explained by each random effect. This method allowed us to decompose the different components of the variance of the LMM model for Magellanic penguin pairs.

Statistical analyses were performed in R (R Core Team 2015; version 3.2.2) and the SIAR package (Parnell and Jackson 2013). Prior to analysis, all data were examined for normality using the Shapiro–Wilk test and homogeneity of variance with Levene Test (Fox and Weisberg 2009). To perform the LMM, we used the ‘lme’ function from ‘nlme’ package (Pinheiro et al. 2015). Significance was assumed at the 0.05 level and all means are presented \pm standard deviation (SD).

Results

Isotope niche

Female Rockhopper penguins differed consistently in isotopic niche position (Euclidean distance, ED) from male and female Magellanic penguins both during the breeding season and the pre-moult (post-breeding) periods in both years studied (Fig. 2; Table 1). The differences in niche position during the breeding season (blood) were due to the lower $\delta^{13}\text{C}$ values for female Rockhopper penguins relative to male Magellanic penguins (all $W=10$, $t \leq 28.061$, $p < 0.001$) as well as to female Magellanic penguins (all $W=0$, $t \leq 133.461$, $p < 0.001$; Fig. 2). Moreover, the differences in niche position were

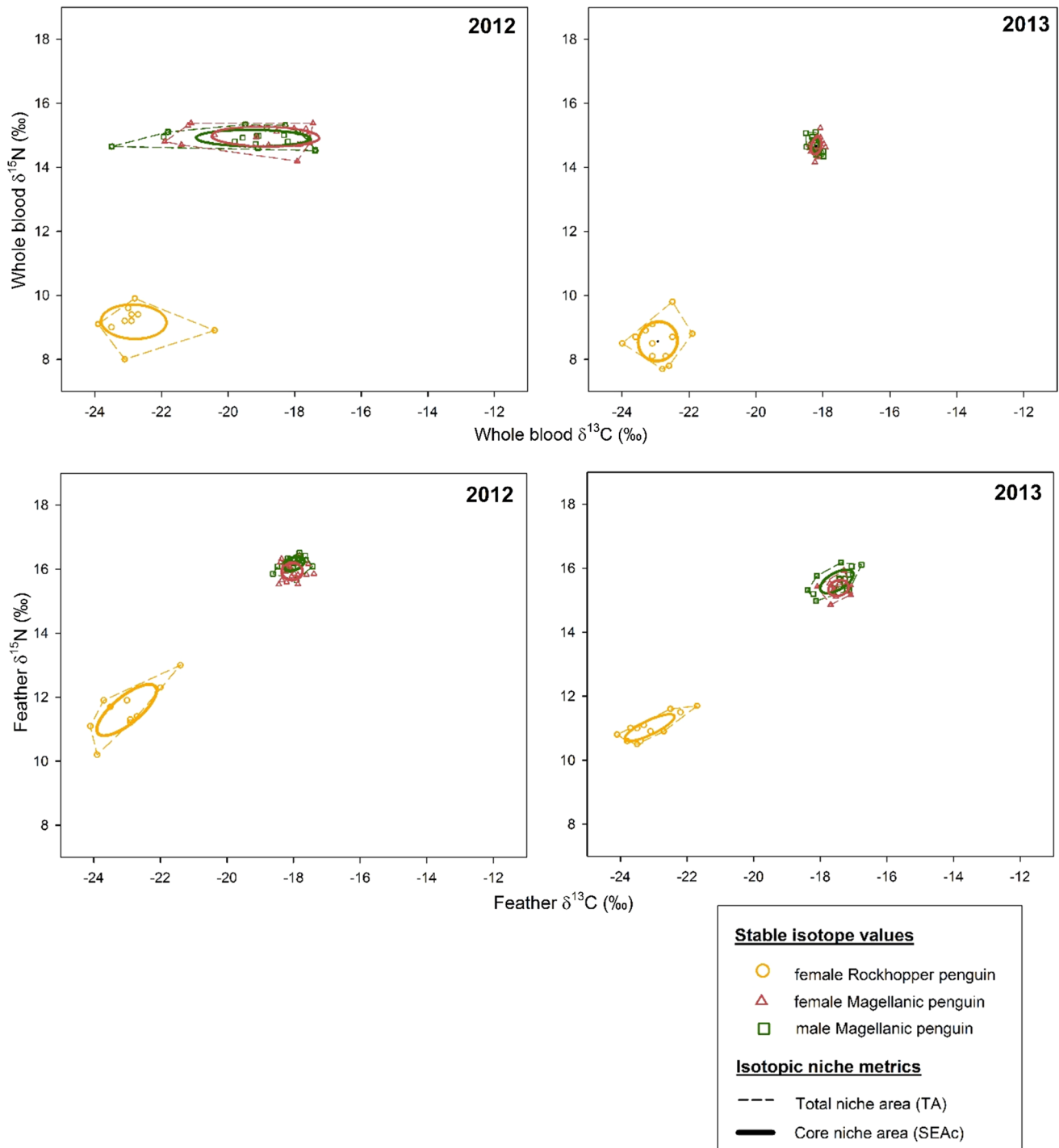


Fig. 2 $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ Bi-plot for whole blood (top) and feathers (bottom) of female Rockhopper penguins (circles), male Magellanic penguins (squares) and female Magellanic penguins (triangles) for the

two years studied (2012 left, 2013 right). Total areas of the isotopic niche are represented by a dotted line and core areas by a continuous line

related to the lower $\delta^{15}\text{N}$ values for female Rockhopper penguin relative to both male Magellanic penguin (all $W=0$, $t \leq |33.77|$, $p < 0.001$) and female Magellanic penguin (all $W=0$, $t \leq |33.48|$, $p < 0.001$; Fig. 2). Niche position did not

differ between male and female Magellanic penguins during the breeding season (Fig. 2; Table 1).

Differences in niche position during the pre-moult period (feathers) were due to the lower $\delta^{13}\text{C}$ values found in female Rockhopper penguins as compared to both male Magellanic

Table 1 Isotopic niche indices for female Rockhopper penguin and male and female Magellanic penguin during the breeding (whole blood) and the post-breeding (feathers) season, for the two years studied

Tissue, year, sex, species	F Rockhopper	M Magellanic	F Magellanic
Whole blood			
2012			
<i>F Rockhopper</i>	–	0	0
<i>M Magellanic</i>	6.77 (< 0.001)	–	1.19 (75.4%)
<i>F Magellanic</i>	7.00 (< 0.001)	0.37 (0.46)	–
2013			
<i>F Rockhopper</i>	–	0	0
<i>M Magellanic</i>	7.72 (< 0.001)	–	0.08 (64.6%)
<i>F Magellanic</i>	7.74 (< 0.001)	0.02 (0.99)	–
Feathers			
2012			
<i>F Rockhopper</i>	–	0	0
<i>M Magellanic</i>	6.80 (< 0.001)	–	0.09 (34.0%)
<i>F Magellanic</i>	6.59 (< 0.001)	0.25 (0.23)	–
2013			
<i>F Rockhopper</i>	–	0	0
<i>M Magellanic</i>	7.24 (< 0.001)	–	0.14 (60.8%)
<i>F Magellanic</i>	7.15 (< 0.001)	0.22 (0.33)	–

Values represent pairwise differences (‰) in the isotopic niche position (Euclidean distance; lower left) and the overlap of core areas (SEAc; upper right) between species/sex groups

F female, *M* male

penguins (all $t \leq |18.25|$, $p < 0.001$) and female Magellanic penguins (all $t \leq |17.9|$, $p < 0.001$; Fig. 2). Furthermore, female Rockhopper penguins had lower $\delta^{15}\text{N}$ values in the pre-moult relative to both male Magellanic penguins (all $t \leq |18.72|$, $p < 0.001$) and female Magellanic penguins (all $t \leq |17.53|$, $p < 0.001$; Fig. 2). Niche position did not differ between male and female Magellanic penguins during the pre-moult period (Fig. 2; Table 1).

Core isotopic niche areas (SEAc) did not overlap among groups (i.e. female Rockhopper penguins, male Magellanic penguins and female Magellanic penguins) in any of the years or stages of the annual cycle studied (Table 1). In general, both core (SEAb) and total (TA) area of the isotope niches were larger in female Rockhopper penguins as compared to male and female Magellanic penguins (Table 2) in the breeding period as well as the pre-moult period. However, there was a large overlap between male and female Magellanic penguin core (SEAc) and total (TA) isotopic niche areas in both the breeding (blood; 65–75%) and the pre-moult (feather; 34–61%) periods of each year (Fig. 2; Table 2).

Based on their 95% confidence intervals, core (SEAb) isotopic niche areas of Rockhopper penguins were similar

between the breeding (blood) and pre-moult (feather) periods in both years examined (Fig. 2; Table 2). However, the total (TA) isotopic niche area of Rockhopper penguins was qualitatively higher during the breeding period in both years (Fig. 2; Table 2). There were no inter-annual differences in Rockhopper penguin SEAb observed during either the breeding or pre-moult period, though TA values during both time periods were qualitatively higher in 2012 relative to 2013 (Table 2).

In 2012, both male and female Magellanic penguins had larger core (SEAb) and total (TA) isotopic niche areas during the breeding period relative to the pre-moult period (Fig. 2; Table 2). In contrast, in 2013 metrics of isotopic niche area for both male and female Magellanic penguins did not differ between the breeding and pre-moult periods (SEAb) or were qualitatively lower during the breeding period (TA; Table 2). During the breeding period core (SEAb) and total (TA) niche areas were larger in 2012 relative to 2013 for both male and female Magellanic penguins (Table 2). However, Magellanic penguin niche area did not differ between years during the pre-moult period for both sexes (Table 2), nor did core (SEAb), or total (TA) niche area differ between sexes between seasons or between years (Table 2).

Intra-specific niche segregation in breeding pairs

During the breeding period (whole blood) 31.5% of the variance in the $\delta^{15}\text{N}$ values of Magellanic penguin pairs was attributed to the differences between years, while the differences among nests was only 8.4% (Table 3). The residual variance (differences within nests) accounted for most of the variance: 60.2% (Table 3). Residual variance (differences within nests) accounted for 96% of the variability in $\delta^{13}\text{C}$ values during the breeding period (whole blood), while differences between years was only 3.0% and differences among nests was only 0.2% (Table 3).

During the pre-moult period (feathers) only 7.8% of the variance in the $\delta^{15}\text{N}$ values of Magellanic penguin pairs was attributed to the variation between years and 0.2% was due to variation among nests (Table 3). The residual variance (difference within nests) accounted for 92.0% of the variance. Males also presented higher $\delta^{15}\text{N}$ values compared to females ($F_{1,32} = 13.79$, $p < 0.001$). During this same time period, differences between years accounted for 54.2% of the variability in $\delta^{13}\text{C}$ values with remaining 45.8% due to residual variance (differences within nests; Table 3).

Individual consistency and specialisation

When comparing regressions with and without the random factor year, we did not find any significant differences (all $L. \text{ratio} \leq |1.32|$, $p > 0.06$). Thus, we discarded

Table 2 Isotopic values for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ (mean \pm SD) in whole blood and feathers, core areas (SEA_b) and total areas (TA) for the three species/sex groups, in the 2 years studied (2012 and 2013)

Sex and penguin species	<i>N</i>	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	SEA_b (‰ ²)	TA (‰ ²)
Blood					
2012					
<i>F Rockhopper</i>	10	-22.8 ± 0.9	9.2 ± 0.5	2.1 (1.3–3.4)	3.4
<i>M Magellanic</i>	18	-19.2 ± 1.7	14.9 ± 0.3	2.2 (1.5–3.2)	3.2
<i>F Magellanic</i>	18	-18.8 ± 1.5	15.0 ± 0.3	2.3 (1.5–3.3)	3.7
2013					
<i>F Rockhopper</i>	12	-22.9 ± 0.6	8.5 ± 0.6	1.6 (1.0–2.4)	2.2
<i>M Magellanic</i>	15	-18.3 ± 0.1	14.7 ± 0.2	0.6 (0.4–0.9)	0.3
<i>F Magellanic</i>	15	-18.3 ± 0.1	14.7 ± 0.3	0.6 (0.4–0.9)	0.3
Feathers					
2012					
<i>F Rockhopper</i>	10	-23.0 ± 0.9	11.6 ± 0.8	2.2 (1.3–3.5)	2.3
<i>M Magellanic</i>	18	-18.0 ± 0.3	16.2 ± 0.2	0.6 (0.4–0.9)	0.6
<i>F Magellanic</i>	18	-18.0 ± 0.3	15.9 ± 0.3	0.6 (0.4–0.9)	0.7
2013					
<i>F Rockhopper</i>	12	-23.1 ± 0.7	11.0 ± 0.4	1.3 (0.8–2.1)	1.0
<i>M Magellanic</i>	15	-17.5 ± 0.5	15.6 ± 0.4	1.0 (0.6–1.4)	1.1
<i>F Magellanic</i>	15	-17.5 ± 0.3	15.4 ± 0.2	0.7 (0.4–1.0)	0.6

For SEA_b , we also present 95% confidence intervals

N sample size, *F* female, *M* male

Table 3 Variance components obtained from LMM (year nested in nestID) for comparison of nesting male–female pairs of Magellanic penguins

Tissue	Variance component	$\delta^{15}\text{N}$			$\delta^{13}\text{C}$		
		Variance (σ^2)	SD (σ)	SD (σ) %	Variance (σ^2)	SD (σ)	SD (σ) %
Blood	Year	0.03	0.18	31.5	0.08	0.28	3.0
	Nest	0.01	0.1	8.4	0.01	0.07	0.2
	Residual	0.06	0.25	60.2	2.55	1.60	96.0
Feathers	Year	0.16	0.39	7.2	0.14	0.37	54.2
	Nest	0.003	0.06	0.2	0.0	0.0	0.0
	Residual	0.07	0.26	92.0	0.12	0.34	45.8

We present the variance and standard deviation for each component and the percent of variance in each of them represent in the overall model

the random term from all regressions performed to simplify the models. Evidence for individual consistency in foraging niche was observed only in the $\delta^{15}\text{N}$ values of female Magellanic penguins ($F_{31} = 6.66$, $p = 0.02$; $r^2 = 0.20$; Fig. 3), suggesting consistency within individuals in relation to the trophic level between stages of the annual cycle. No significant relationships were found between tissue $\delta^{15}\text{N}$ values for male Magellanic penguins ($F_{31} = 4.06$, $p = 0.06$, $r^2 = 0.11$; Fig. 3) or female Rockhopper penguins ($F_{20} = 0.81$, $p = 0.38$, $r^2 = 0.04$; Fig. 3). There were no significant relationships between the $\delta^{13}\text{C}$ values of whole blood and feathers for female Magellanic penguin ($F_{31} = 3.05$, $p = 0.09$, $R^2 = 0.09$), male Magellanic penguins ($F_{31} = 0.58$, $p = 0.45$, $R^2 = 0.02$) or female Rockhopper penguin ($F_{20} = 0.001$, $p = 0.98$, $R^2 = 0$).

Discussion

Our results indicate seasonally persistent inter-specific foraging niche segregation between sympatric female Rockhopper penguins and male and female Magellanic penguins during the breeding and the pre-moult periods. This suggests that adult penguins of both species differentiate foraging areas and trophic position even once the chicks fledge and they are no longer constrained to their parental duties. Carbon stable isotope values suggested that female Rockhopper penguins consistently foraged in more oceanic/pelagic habitats (lower $\delta^{13}\text{C}$ values) while Magellanic penguins foraged in more coastal/benthic habitats (higher $\delta^{13}\text{C}$

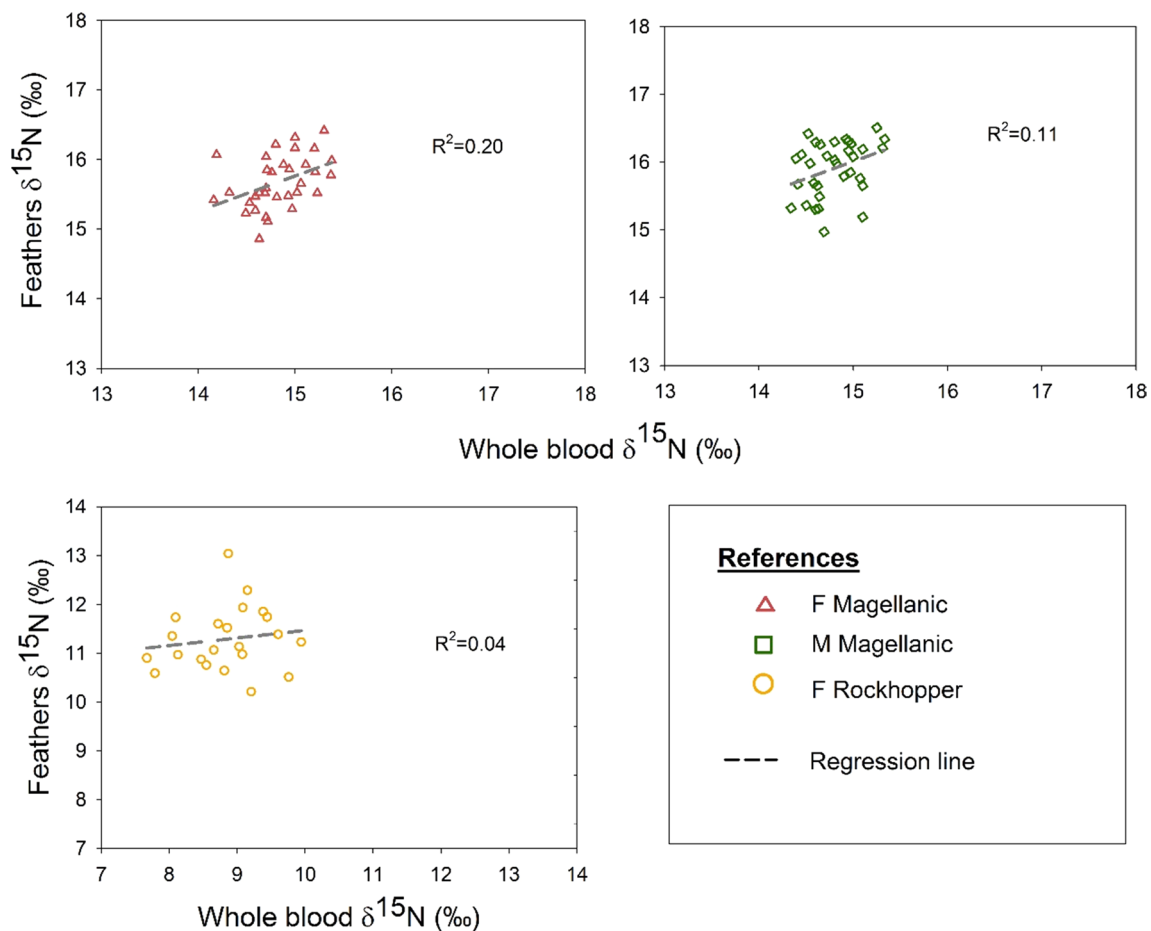


Fig. 3. Individual consistency in trophic level ($\delta^{15}\text{N}$) during the breeding and the post-breeding season (whole blood and feathers, respectively) for the three species/sex group studied. R^2 values are

presented on the graphs. Only female Magellanic penguins presented a significant positive relationship

values). In addition, nitrogen stable isotope values suggest that female Rockhopper penguins consistently fed at a lower trophic position (low $\delta^{15}\text{N}$ values) as compared to male and female Magellanic penguins during both the breeding and the pre-moult periods.

Past studies of the foraging ecology of these two sympatric penguin species at Isla de los Estados have been focused on the breeding season when individuals are constrained to forage near their colonies. The data from GPS tracking, time depth recorders and stable isotope analyses indicated that during the breeding season both species were highly segregated in the spatial areas used to forage (vertical and horizontal axes) and trophic position (Rosciano et al. 2016). We expected that niche segregation would relax and consequently foraging niches would widen once the breeding season is over, if the differences observed by Rosciano et al. (2016) were a reflection of a perceived high potential for competition during the breeding season. However, our results suggest that observed inter-specific differences in foraging niches are persistent outside of the breeding season

as well. Our results are supported by studies of sympatric Rockhopper and Magellanic penguin species at the Falkland/Malvinas Islands during the pre-moult period, which found that Rockhopper penguins had lower $\delta^{15}\text{N}$ values relative to Magellanic penguins (Weiss et al. 2009; Dehnhard et al. 2011). However, unlike our results at Isla de los Estados, Rockhopper and Magellanic penguins from the Falkland/Malvinas Islands had similar $\delta^{13}\text{C}$ values, suggesting a large overlap in the foraging areas between species during the pre-moult period (Weiss et al. 2009; Dehnhard et al. 2011).

Conventional dietary studies performed on Rockhopper and Magellanic penguins in the study area or proximate colonies also support our stable isotope-based results. For example, small crustaceans, such as *Euphysiids* and *Themisto* sp. are abundant in Rockhopper penguin diets while Magellanic penguins fed preferentially on fish (Thompson 1993; Pütz et al. 2001; Raya Rey and Schiavini 2005; Scioscia et al. 2014). In addition, direct tracking data indicates very little overlap between species' foraging areas during the breeding period at Isla de los Estados (Rosciano et al. 2016).

Moreover, at the Falkland/Malvinas Islands, sympatric Rockhopper and Magellanic penguins also showed strong spatial and dietary segregation during the breeding season, with Rockhopper penguins always foraging on lower trophic-level prey items as compared to Magellanic penguins (Masello et al. 2010). Although these species have not been directly tracked at Isla de los Estados during the pre-moult foraging period, their stable isotope values suggest that during the pre-moult period penguins continue to use the same foraging habitat types used while breeding. This result contrasts with our initial expectation that foraging habitat partitioning would be relaxed during the pre-moult period when adults are less restricted in their foraging range and trip duration.

When comparing the isotopic niche position of female Rockhopper penguins between the breeding and pre-moult periods, we found a small shift towards higher $\delta^{15}\text{N}$ values in the pre-moult periods, relative to the breeding period. This may indicate that female Rockhopper penguins feed at higher trophic levels outside of the breeding period. However, we did not normalize tissue stable isotope values for trophic discrimination to facilitate direct comparison between tissues and thus seasons (Cherel et al. 2005a). Even so, the differences observed between the $\delta^{15}\text{N}$ values of whole blood and feathers would be evident at the same magnitude even with the application of a discrimination factor (e.g. Dehnhard et al. 2011).

Female Rockhopper penguins generally had larger core (SEA_b) and total (TA) isotopic niches areas as compared to male and female Magellanic penguins, with the exception of the breeding season in 2012. This implies greater intra-specific variability and the use of a wider range of trophic position and foraging habitats used by female Rockhopper penguins (Ceia et al. 2014; Polito et al. 2015; Herman et al. 2017). This is an important characteristic for the species due to their conservation status of 'vulnerable' (IUCN; Birdlife International 2012). Populations that present a higher variability among individuals, have a greater capacity of adapting to changes that may occur in the environment (Bolnick et al. 2003). For instance, among *Pygoscelid* species, Gentoos penguins (*P. papua*) have shown the most generalist foraging strategy, improving their adaptability to environmental changes occurring within their breeding areas in the Antarctic Peninsula (Miller et al. 2009; Polito et al. 2015; Herman et al. 2017).

We found little evidence of sex-specific foraging niche segregation between male and female Magellanic penguins at Isla de los Estados. The core (SEA_b) and total (TA) isotopic niche areas of male and female Magellanic penguins in our study were similar in size and overlapped between sexes during both the breeding (65–75%) and pre-moult (34–61%) periods. When comparing foraging niches within breeding pairs of Magellanic penguins, we observed variability in

$\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values within the same nest although differences within pairs were not consistent. One exception to this trend is that individual male Magellanic penguins feed at slightly higher trophic positions (i.e. higher $\delta^{15}\text{N}$ values) as compared to their female mates during the pre-moult period. This indicates that while sex-specific differences in foraging niche may not be apparent at the population level, the potential for small differences within pairs exists during some periods in their annual cycle. Even so, there was no evidence of sex-specific foraging niche segregation during the breeding period when pairs are central-place foragers and the potential for competition for food resources is likely higher.

In contrast, a prior study of Magellanic penguins in northern Patagonia found that female isotopic niches were always encompassed by male isotopic niches during the pre-moult period (Silva et al. 2014). In addition, males in northern Patagonia exhibited a larger isotopic niche area relative to females, which was interpreted as males consuming a broader variety of prey types and using a wider range of foraging habitat during the pre-moult period (Silva et al. 2014). Silva et al. (2014) further suggested that differences in diving capacity for both sexes led to the observed isotopic niche variation, since differences in the diving depths explored were observed for Magellanic penguins at different stages of the breeding season (e.g. early chick rearing and incubation, Walker and Boersma 2003; Raya Rey et al. 2012). However, a recent tracking study at Isla de los Estados found no sex-specific differences in foraging dive depths explored or foraging areas during the breeding season (Rosciano et al. 2018). The differences observed between locations in the degree of sex-specific niche differentiation could be due in part to differences in prey availability. For example, higher prey availability at Isla de los Estados could relax the potential for intra-specific competition (Sánchez et al. 1995; Hansen 1999).

Correlations between the stable isotope values of tissues synthesised at distinct time periods are commonly used to infer the degree of individual consistency in foraging niches across seasons (e.g. Ceia et al. 2012). Using this approach, we did not find evidence of individual consistency in trophic position ($\delta^{15}\text{N}$ values) or foraging habitat use ($\delta^{13}\text{C}$ values) within female Rockhopper penguins and male Magellanic penguins between the breeding and pre-moult period. However, female Magellanic penguins exhibited some individual consistency in trophic position ($\delta^{15}\text{N}$ values) between the breeding and pre-moult periods (see Fig. 3), which is worth further exploration. The lack of consistency in $\delta^{13}\text{C}$ values between the breeding (blood) and pre-moult (feathers) periods (see 'Individual consistency and specialisation' on the Result section) in female Rockhopper penguins and Magellanic penguins of both sexes suggests that individuals within the population may vary in their use of distinct water masses

inside and outside of the breeding periods (e.g. more oceanic waters during the breeding season and coastal waters during pre-moult or vice versa).

Our study focused on exploring individual consistency in foraging niches between seasons (e.g. consistent between individual differences in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values when comparing between the breeding and pre-moult periods). However, since we did not resample the same individuals in each year, we could not explore individual consistency within the breeding and pre-moult periods between different years. However, a previous study found that individual female Southern Rockhopper penguins from the Falkland/Malvinas Islands had consistent foraging niches across years during the pre-breeding period but not during the pre-moult period, suggesting a switch between foraging strategies between periods of the life cycle (Dehnhard et al. 2016). Our results support the conclusions of Dehnhard et al. (2016) and re-emphasise that the degree of individual foraging specialisation in female Rockhopper penguins and possibly Magellanic penguins, is likely to vary both seasonally (between seasons) and annually (within season across years).

Conclusions

In this study, we used carbon and nitrogen stable isotope analysis of whole blood and feathers to assess inter- and intra-specific variation in the foraging niches of sympatric female Southern Rockhopper penguin and male and female Magellanic penguins. Our results indicate that inter-specific foraging niche segregation is seasonally persistent during the breeding period as well as the post-breeding, pre-moult period. In addition, we found little evidence of sex-specific or individual differences in foraging niches within or between the breeding and pre-moult periods. The results suggest that inter-specific differences have a stronger influence on the foraging behaviours of sympatric Southern Rockhopper and Magellanic penguins at Isla de los Estados, relative to intra-specific factors. Even so, these results differ from our initial hypothesis that inter-specific foraging niche segregation would be relaxed outside of the breeding season once adults are released from central-place foraging and the potential for competition is likely reduced. This suggests that, either the potential for inter-specific competition for food or foraging areas remains high outside of the breeding season or that the ultimate factors responsible for foraging niche segregation among these two species may be unrelated to these proximate factors. For example, Trivelpiece et al. (1987) proposed that ecological segregation among sympatric penguins in the genus *Pygoscelis*, are the result of adaptations by each species to the major environmental conditions found at the centre of their respective geographical ranges

and not competition per se. Future work that quantifies diets, prey availability and foraging areas of sympatric Southern Rockhopper and Magellanic penguins throughout their annual cycle is warranted to identify the ultimate factors responsible for their observed foraging niche segregation.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflicts of interest.

Human and animal ethics All applicable international, national and/or institutional guidelines for the care and use of animals were followed and all necessary approvals have been obtained.

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