

Do penguins share? Evidence of foraging niche segregation between but not within two sympatric, central-place foragers

N. G. Rosciano^{1,*}, M. J. Polito², A. Raya Rey^{1,3}

¹Ecología y Conservación de Vida Silvestre, Centro Austral de Investigaciones Científicas, Consejo Nacional de Investigaciones Científicas y Técnicas, Bernardo A. Houssay 200 (V9410CAB), Ushuaia, Tierra del Fuego, Argentina

²Department of Oceanography and Coastal Sciences, Louisiana State University, Baton Rouge, LA 70803, USA

³Universidad de Tierra del Fuego, Darwin s/n, 9410 Ushuaia, Tierra del Fuego, Argentina

ABSTRACT: Niche theory predicts that sympatric species should differentiate ecologically in order to co-exist and conspecifics will also differentiate to reduce intra-specific competition. As central-place foragers, colonial breeding seabirds represent an ideal model system to test this theory and examine the mechanism of niche segregation. We used GPS-TDlog devices for tracking and diving data and stable isotope analysis to examine patterns of inter- and intra-specific niche segregation among southern rockhopper penguins *Eudyptes chrysocome chrysocome* and Magellanic penguins *Spheniscus magellanicus* breeding on Isla de los Estados, Argentina, across 3 consecutive breeding seasons. Tracking data indicated strong inter-specific spatial segregation of foraging locations and little overlap. Diving data also highlighted vertical foraging niche segregation as female rockhopper penguins dove deeper than male and female Magellanic penguins. $\delta^{13}\text{C}$ values supported the general pattern of habitat segregation, with lower values for female rockhopper penguins that dove deeper and foraged off the shelf break. Female rockhopper penguins exhibited a lower relative trophic value ($\delta^{15}\text{N}$) than male and female Magellanic penguins, consistent with previous dietary studies of both species. These differences likely act to reduce competition between the 2 species during the breeding season, when they are constrained to exploit the resources around their colonies. In contrast, male and female Magellanic penguins shared a similar foraging niche as measured by areas used to forage, dive depths, relative habitat use and trophic values. The lack of sex-specific foraging niche segregation of Magellanic penguins at Isla de los Estados could be related to the availability of food in the area and/or the small population size.

KEY WORDS: *Eudyptes chrysocome chrysocome* · *Spheniscus magellanicus* · Stable isotopes · Niche partitioning · Isla de los Estados

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INTRODUCTION

The ecological niche is defined as the functional role of an organism in its community, focusing especially on trophic relationships with other species (Elton 1927). Hutchinson (1957) added to this concept the idea of niche width, defined as the total variety of resources exploited by an organism, which in prac-

tice is usually narrower than what organisms can potentially exploit due to the presence of competitors. As such, a central aspect of studies focused on ecological niche theory concerns the assessment of the amount of resource sharing (i.e. niche overlap) between and within species. This is because the principle of competitive exclusion predicts that similar species cannot co-exist in the long-term in

*Corresponding author: natirosciano@yahoo.com

the absence of ecological differences (Lewis et al. 2001). Therefore, sympatric species generally evolve morphological and/or behavioral characteristics that act to differentiate these species along one or more ecological-niche axes (Hutchinson 1957). As the potential for intra-specific competition can often be higher than competition among congenetics, niche segregation can also occur between conspecifics (Begon et al. 2006).

Seabirds are often used as model organisms to study inter-specific and intra-specific niche segregation (e.g. Lewis et al. 2001, Polito et al. 2015). During the breeding season seabirds act as central-place foragers given that they are constrained to only exploit resources within a foraging range around their colonies or nest (Costa 1991, Grémillet et al. 2004). As most seabirds nest in large, often mixed-species breeding colonies and forage in environments with temporally or spatially limited resources, the potential competition for food between and within species can be high unless foraging niche segregation occurs. Relying on different food resources, using different foraging habitats, areas or depths, and/or differentiating peak resource or habitat use, can all act to segregate foraging niches and reduce competition between and within breeding seabirds (Croxall & Prince 1980, Lewis et al. 2001, Raya Rey et al. 2013, Quillfeldt et al. 2015). Even so, while ecological models predict the potential for absolute partitioning (Cairns 1989), empirical studies often highlight only partial niche segregation between and within species, possibly due to variability in the abundance of available food resources (Sapozhnikow & Quintana 2003, Wilson 2010, Ratcliffe et al. 2014), as well as ontogenetic or age-based segregation within species (Forero et al. 2002, Pelletier et al. 2014).

Stable isotope analysis is a tool widely used to provide information on trophic ecology and assess patterns of habitat use by organisms (Hobson 2005, Newsome et al. 2012). In marine systems, stable carbon isotope values ($\delta^{13}\text{C}$) reflect primary carbon sources within a food web and can be used to trace trends in marine habitat use by consumers (inshore/benthic vs. offshore/pelagic; Cheral & Hobson 2007). Stable nitrogen isotope values ($\delta^{15}\text{N}$) reflect the trophic position of consumers due to a step-wise enrichment of ^{15}N between trophic levels (Minagawa & Wada 1984). When presented as bi-plots, $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values act to delineate an animal's 'isotopic niche' (Newsome et al. 2007). The isotopic niche approach provides quantitative information on resource and habitat use, parameters that can be used as prox-

ies to define the ecological niche of individuals, populations and/or species (Hutchinson 1957). Metrics can be obtained from the isotopic niche of a population, such as the total niche area, width and position, allowing researchers to compare niche overlap and segregation within and between community members (Turner et al. 2010, Jackson et al. 2011, Layman et al. 2012).

Complementary to stable isotope analysis, direct tracking of seabird movements over time and space can identify patterns of spatial and temporal foraging niche segregation within and between species (Ratcliffe et al. 2014). In addition, devices that simultaneously register location as well as dive depth data provide the potential to reconstruct the horizontal and vertical movements of diving seabirds (Masello et al. 2010, Raya Rey et al. 2012b). Combining direct tracking with stable isotope analyses allows for simultaneous examination of resource and foraging area utilization to quantify niche partitioning in seabirds (Masello et al. 2010, Hinke et al. 2015). For example, while 2 or more species of diving seabirds may forage in the same area, the preferential use of different depths can act to reduce competition and explain how species co-exist using the same resources (Wilson 2010).

In this context, the goal of our study was to examine patterns of inter- and intra-specific foraging niche segregation in 2 penguin species breeding on Isla de los Estados, Argentina. These 2 species, the southern rockhopper *Eudyptes chrysocome chrysocome* (hereafter 'rockhopper') and Magellanic *Spheniscus magellanicus* (hereafter 'Magellanic') penguins breed in sympatry on Isla de los Estados (Raya Rey et al. 2014) where they are central-place foragers during the whole breeding season. Guard stage foraging trips begin in late November, when chicks start hatching, and it becomes critical that parents feed them regularly (Warham 1975, Boersma et al. 1990). While several studies have examined the foraging ecology of these 2 species in isolation (Schiavini & Raya Rey 2004, Wilson et al. 2005, Ciancio et al. 2015), the few that examined their respective foraging niches in sympatry are focused on a single geographic area (i.e. the Malvinas/Falkland Islands; Pütz et al. 2001, Weiss et al. 2009, Masello et al. 2010).

As such, we evaluated foraging niche partitioning among rockhopper and Magellanic penguins and between sexes for Magellanic penguins, during the early chick rearing period over 3 consecutive breeding seasons (2011–2013) using direct tracking and stable isotope analyses. Based on previous conven-

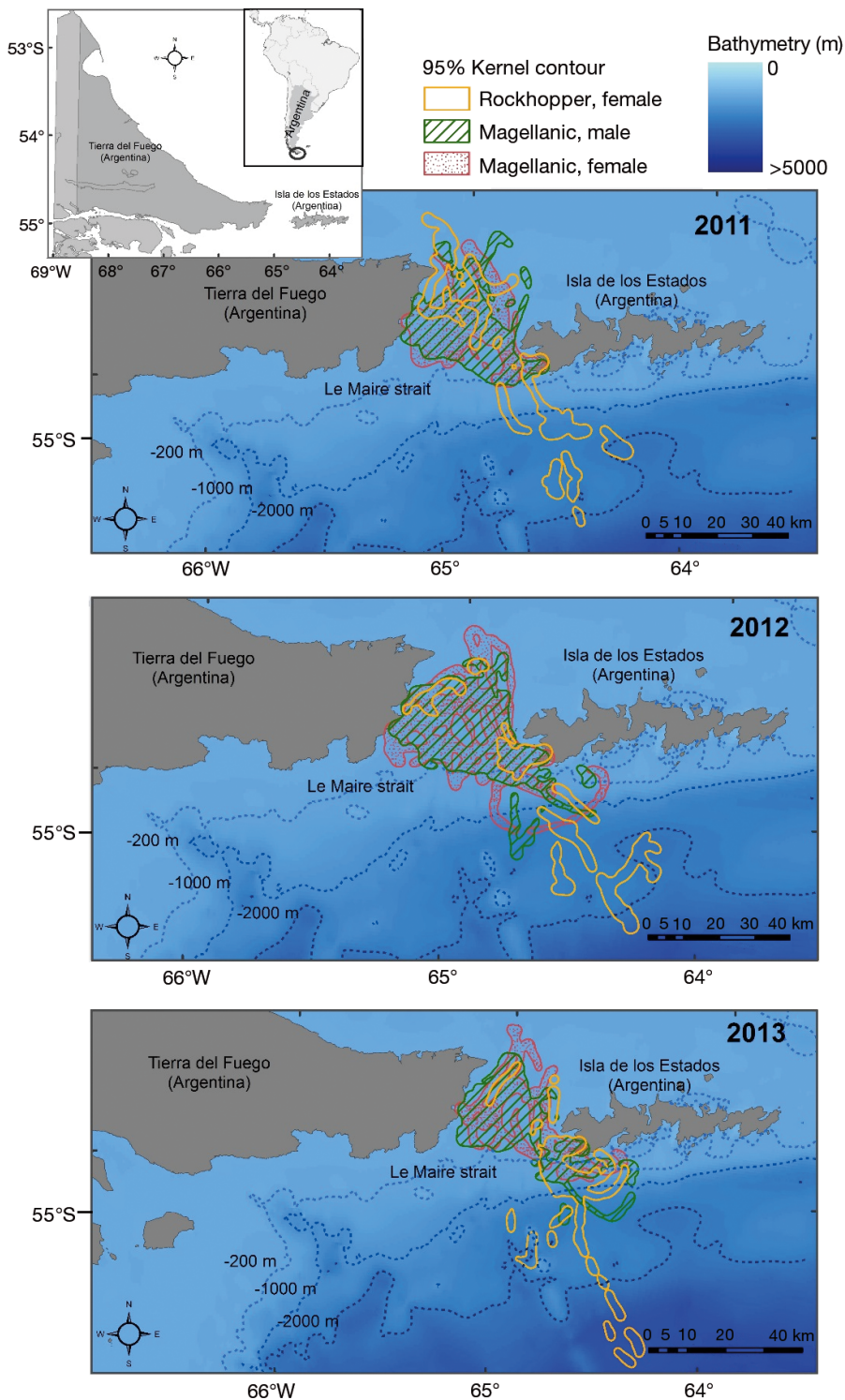


Fig. 1. Study area and foraging ranges. Inset: Tierra del Fuego Island and Isla de los Estados, Argentina. The 3 main panels show space segregation of female rockhopper penguins *Eudyptes chrysocome chrysocome* and male and female Magellanic penguins *Spheniscus magellanicus* in the 3 years studied. 95% kernel density distribution reflects the foraging ranges at sea used by the seabirds, and the overlap between species/sex groups (see map key)

tional dietary studies of these species we predict inter-specific segregation in isotopic niche space ($\delta^{15}\text{N}$) between species due to the likely differences in the trophic level of preferred prey resources (Raya Rey & Schiavini 2005, Scioscia et al. 2014). It is also likely that these 2 species may exhibit some degree of horizontal (foraging area) or vertical (foraging depth) segregation in their respective foraging niches due to different areas or depths where prey occur, which we test using direct tracking and isotopic values ($\delta^{13}\text{C}$; Cherel & Hobson 2007, Masello et al. 2010). In addition, Magellanic penguins present sexual dimorphism in body size, with males being 5 to 15% larger than females (Agnew & Kerry 1995, Forero et al. 2001, Raya Rey et al. 2013), that has been previously associated with differences in diets (Forero et al. 2002) and some diving parameters (e.g. males dive deeper and for longer; Walker & Boersma 2003, Raya Rey et al. 2012b) at other colonies. Therefore we also expect to find intra-specific differences in foraging niches used by Magellanic penguins of different sexes at Isla de los Estados.

MATERIALS AND METHODS

Study area, species and colony locations

The study area is located in Isla de los Estados, on the east side of Tierra del Fuego archipelago, Argentina, at the southernmost end of South America ($54^{\circ}55'S$, $64^{\circ}46'W$; Fig. 1). The island is separated by 30 km from Tierra del Fuego by the Le Maire Strait and is included within the Argentine continental shelf; it has a surface area of 520 km^2 (Ponce & Fernández 2014 and references therein). Isla de los Estados is one of the most important breeding grounds for the southern rockhopper penguin *Eudyptes chrysocome chrysocome* (Schiavini

2000), holding around 130 000 breeding pairs, the majority located in our study site, Franklin Bay (Raya Rey et al. 2014). The Magellanic penguin *Spheniscus magellanicus* colony we examined in this study was located nearby on the southwestern side of Franklin Bay and has approximately 1600 breeding pairs (Raya Rey et al. 2014).

Field-work and sample collection

We conducted field-work from the end of November to mid-December, during the early chick-rearing period of the breeding season, in 3 consecutive years (2011, 2012 and 2013). We randomly selected breeding adult Magellanic and rockhopper penguins that were found attending active nests. For Magellanic penguins, we sampled male and female because both sexes trade-off feeding chicks during the early chick rearing period (Boersma et al. 1990). We sampled only adult female rockhopper penguins because females forage at sea and feed their chicks during the early chick rearing period, while male rockhopper penguins remain at the nest to guard the chicks (Warham 1975).

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 calipers (to the nearest 0.02 mm) to determine sex (Gandini et al. 1992, Hull 1996). Afterwards, we equipped adults with GPS-TDlog devices (size: $11.6 \times 3.5 \times 2$ cm for Magellanic penguins, $5.6 \times 3.1 \times 1.5$ cm for rockhopper penguins; Earth & Ocean Technology). Following Wilson et al. (1997; their Method 2), we attached the devices along the midline of the penguin's back using black tape (Tesa, Beiersdorf AG) subsequently covered with a layer of quick-drying epoxy glue to prevent the birds from removing the tape with their bills, taking at most 20 min per bird due to the cold weather and the difficulty to dry the epoxy. We programmed the GPS-TDlogs to register temperature and depth every 2 s and latitude and longitude positions every 2 min, to record one foraging trip per equipped penguin.

We re-captured the penguins at their nests when they returned to the colony following a foraging-at-sea trip. We recovered the GPS-TDlog devices and collected whole blood samples in microcapillary tubes (approximately 75 μ l) for stable isotope analysis. We took the blood sample from each equipped individual using a sterile needle and venipuncture of the tarsal vein. We preserved the blood samples in

70% ethanol until processing in laboratory. Previous studies have shown little effect of alcohol preservation on blood of birds and other organisms (Hobson et al. 1997).

GPS data analyses

We analysed the GPS tracking data recovered from the GPS-TDlogs, using ArcGIS 9.3.1 together with Hawth's Analysis Tools (www.spatalecolology.com/htools). We estimated for each individual the maximum foraging distance (km) reached from the breeding colony. We then used 3 separate linear models (LM) to test for differences in this response variable (maximum foraging distance) between our species/sex groups (female rockhopper penguins, male Magellanic penguins and female Magellanic penguins) within each year studied (2011, 2012 and 2013). If we obtained significant differences between groups (species/sex), we performed a post-hoc test. We used least-square means analysis (LS means) for pairwise comparisons between groups, with $\alpha = 0.05$, using the package 'lsmeans' for R (Lenth & Herve 2015).

In addition, we used kernel density estimation analysis to quantify the foraging areas used by the 3 penguin groups in each year. We calculated 95% kernel contours for each group in each year, which are indicative of the areas that contain $x\%$ of the volume of a probability density distribution. We interpret 95% kernel areas as representative of overall foraging distribution of each penguin group. We then used the intersect tool of ArcGis to calculate the degree of inter-specific overlap in the estimated kernel areas among groups.

Diving data analysis

We analysed penguin diving data recovered from the GPS-TDlogs, using Multitrace Software (Jensen Software Systems) following the method of Raya Rey et al. (2012b). From this diving data we extracted the maximum dive depth (m) and average dive depth (m) obtained for each individual across all dives. In addition, we examined the values of these 2 dive metrics for each individual after filtering to obtain only dives that contained wiggles, which are commonly associated with prey capture and ingestion (Simeone & Wilson 2003, Hanuise et al. 2010).

We then used 3 separate LM to test for differences in each diving metric among our species/sex groups (female rockhopper penguins, male Magellanic pen-

guins and female Magellanic penguins) within each year studied (2011, 2012 and 2013). If we obtained significant differences between groups (species/sex), we performed a post-hoc test. We used LS means analysis for pairwise comparisons between groups, with $\alpha = 0.05$, using the package 'lsmeans' for R.

Stable isotope analysis

Prior to analyses, we dried whole blood samples in an oven at 60°C and then freeze-dried samples in a lyophilizer. We weighed out ~0.5 mg of each sample into tin cups that were then flash-combusted (Cotech ECS4010 or PDZ Europa ANCA-GSL elemental analyzers) for carbon and nitrogen isotope analysis ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) through an interfaced continuous-flow stable isotope ratio mass spectrometer (Thermo Scientific Delta V Plus or PDZ Europa 20-20). Sample precision based on 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:

$$\delta X = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1000 \quad (1)$$

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. 2005, Hedd & Montevicchi 2006).

Isotopic niche analysis

We sampled whole blood from breeding adults of both species during the early chick-rearing period when the chicks ranged from 1 to 4 wk of age. A recent controlled dietary study indicates that the isotopic whole-blood values in adult penguins provide dietary information averaged over a period of approximately 20 d (Barquete et al. 2013). Therefore, the isotopic data examined in our study integrates the dietary history of adults primarily during the early chick-rearing period, but may also include a portion of the late incubation period for both species of penguins.

We used the isotopic niche approach (Newsome et al. 2007) to compare foraging niche position, width,

and overlap between penguin groups (species/sex). Following the methods of Hammerschlag-Peyer et al. (2011) we used both multivariate ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) and univariate ($\delta^{13}\text{C}$ or $\delta^{15}\text{N}$) techniques to identify and assess the degree of inter-specific isotopic niche partitioning.

First we tested for differences in isotopic niche position among penguin groups by computing the Euclidean distance (ED) between group centroids ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$), following the methods of Turner et al. (2010). Isotopic niche positions were considered different if the ED between 2 groups or years was >0 after comparison with null distributions generated by a residual permutation procedure. A difference in this central tendency represents a shift in the isotopic niche position between the groups examined. If significant differences between niche positions (ED) were identified using this multivariate approach, we then used the t -test for independent samples (for normally distributed data) or the Wilcoxon test (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 (Hammerschlag-Peyer et al. 2011).

Next, we tested for differences in niche area and overlap among penguin groups using standard ellipse areas corrected for small sample size (SEAC; Jackson et al. 2011). The SEAC can be interpreted as the core isotopic foraging niche of a population (Polito et al. 2015). In addition, 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 characterization of the population niche (Layman & Allgeier 2012). We also calculated mean distance to centroid (MDC; Turner et al. 2010), which is a measure of the distance of each individual to the mean distance of all individuals in isotopic space and acts as a measure of a population's foraging niche width (Layman et al. 2007). Using an analysis of nested linear models and residual permutation procedures, the absolute value of MDC differences was evaluated among groups and across years, with absolute values >0 indicating a significant difference in niche width (Turner et al. 2010). If differences in MDC were found, we used Bartlett's test to determine which axis ($\delta^{13}\text{C}$ or $\delta^{15}\text{N}$) was contributing to the observed differences in isotopic niche width (Hammerschlag-Peyer et al. 2011). Last, we measured pairwise niche overlap between penguin groups or years by quantifying the percentage of individuals in each group or year that were

Table 1. Number of penguins equipped with GPS-TDlog devices in the 3 years studied, dive data and GPS data recovered for each year, and number of whole blood samples taken from female (F) rockhopper penguins *Eudyptes chrysocome chrysocome* and male (M) and female Magellanic penguins *Spheniscus magellanicus*

Penguin species and sex	Equipped	Data recovered		Whole blood sampled
		Dives	GPS	
2011				
Rockhopper F	13	12	9	12
Magellanic M	10	8	8	9
Magellanic F	11	8	8	11
2012				
Rockhopper F	10	4	9	10
Magellanic M	9	2	9	9
Magellanic F	9	3	9	9
2013				
Rockhopper F	13	11	11	12
Magellanic M	7	6	6	7
Magellanic F	8	8	8	8

encompassed by a comparison group or year's SEAc or TA to obtain measures of core and total isotopic niche overlap (Hammerschlag-Peyer et al. 2011).

All statistical analyses were performed in R software ver. 3.1.2 (R Core Team 2015) and the SIAR package (ver. 4.2; Parnell & Jackson 2013). Prior to analysis, all data were examined for normality using the Shapiro-Wilks test and square-root transformed when necessary, and examined for homogeneity of variance using Levene's test (CAR package; Fox & Weisberg 2009). Significance was assumed at the $\alpha = 0.05$ level and all means are presented \pm SD.

RESULTS

After the 3 seasons of deployment, we successfully recovered location (GPS) data, diving data and whole blood samples from female rockhopper penguins and male and female Magellanic penguins as given in Table 1. Differences in data recovered for tracking and diving data were due to logger failure.

GPS data

Both species foraged across the Le Maire Strait, near the shores of Tierra del Fuego Island, as well as the areas to the southeast of Isla de los Estados (Fig. 1). Only female rockhopper penguins foraged in areas further south and off-shore from the shelf

break (Fig. 1). As such, foraging area overlapped little between species, ranging from 14.3 to 35.0% between female rockhopper penguins and male Magellanic penguins and 13.3 to 32.8% between female rockhopper penguins and female Magellanic penguins across the 3 years of our study (Table 2). This small overlap area was due to 3 Magellanic penguins that foraged to the southeast of Isla de los Estados in both 2012 and 2013 as well as 5 female rockhopper penguins that were tracked near the shores of Tierra del Fuego in 2011 and 2013 (Fig. 1). In contrast, intra-specific overlap in foraging areas was higher, with overlap between male and female Magellanic penguins ranging from 67.5 to 73.3% across the 3 years of our study (Table 2). Maximum distance to the colony did not differ between or within species in any of the 3 years studied (LM: 2011: $F_{18} = 0.69$, $p = 0.51$; 2012: $F_{24} = 0.67$, $p = 0.52$; 2013: $F_{20} = 0.19$, $p = 0.19$; Table 3).

Diving data

When examining all diving events, maximum dive depths obtained by individuals differed significantly among the 3 species/sex groups in 2013 ($F_{22} = 5.28$, $p = 0.01$) with both female rockhopper and male Magellanic penguins performing deeper maximum dives than female Magellanic penguins (Table 3).

Table 2. At-sea foraging area overlap between rockhopper and Magellanic penguin species/sex (F: female; M: male) groups, in the 3 years studied. 95% kernel contours were calculated for each species/sex group in each year. Values represent the percentage of the 95% kernel contour that overlapped between each species/sex group in each year. 95% kernel contours are interpreted as the overall foraging distribution

Penguin species and sex	95% kernel overlap (%)		
	Rockhopper F	Magellanic M	Magellanic F
2011			
Rockhopper F	–	25.5	25.8
Magellanic M	14.3	–	73.3
Magellanic F	13.3	67.5	–
2012			
Rockhopper F	–	16.5	13.8
Magellanic M	35.0	–	8.2
Magellanic F	32.8	72.9	–
2013			
Rockhopper F	–	24.1	22.8
Magellanic M	32.1	–	50.2
Magellanic F	23.6	64.4	–

Table 3. GPS and dive data used to compare between rockhopper and Magellanic penguin species/sex groups (F: female; M: male). Data was obtained from the GPS/TDlogs deployed on penguins. Values presented are mean \pm SD. Differences between species/sex groups were tested with linear models. Different letters indicate significant differences within years after Tukey's HSD post-hoc test ($\alpha = 0.05$)

Penguin species and sex	— GPS data —	— All dives —		— Dives with wiggles only —	
	Max. distance to colony (km)	Max. depth (m)	Mean depth (m)	Max. depth (m)	Mean depth (m)
2011					
Rockhopper F	39.87 \pm 11.55	65.39 \pm 11.09	19.79 \pm 8.22 ^b	59.80 \pm 14.90 ^b	33.15 \pm 11.07 ^b
Magellanic M	34.48 \pm 8.95	68.85 \pm 11.52	15.91 \pm 6.32 ^{ab}	56.84 \pm 19.19 ^{ab}	29.70 \pm 11.89 ^{ab}
Magellanic F	32.50 \pm 12.66	54.94 \pm 13.41	9.90 \pm 3.42 ^a	37.41 \pm 18.70 ^a	20.00 \pm 9.32 ^a
2012					
Rockhopper F	29.43 \pm 15.11	61.92 \pm 14.97	15.12 \pm 4.77	53.80 \pm 22.68	24.50 \pm 14.74
Magellanic M	32.95 \pm 7.12	76.29 \pm 9.12	14.26 \pm 7.13	42.66 \pm 28.29	17.63 \pm 11.50
Magellanic F	35.18 \pm 7.62	67.95 \pm 23.12	10.94 \pm 5.41	46.69 \pm 7.91	24.03 \pm 8.52
2013					
Rockhopper F	21.31 \pm 19.14	69.05 \pm 9.62 ^b	12.98 \pm 4.99 ^b	47.49 \pm 21.11 ^b	20.80 \pm 12.33
Magellanic M	21.60 \pm 14.39	72.66 \pm 11.91 ^b	6.58 \pm 1.71 ^a	51.34 \pm 14.80 ^b	23.28 \pm 3.98
Magellanic F	26.97 \pm 13.16	50.22 \pm 20.89 ^a	6.19 \pm 2.05 ^a	16.45 \pm 12.48 ^a	10.68 \pm 7.25

There was no difference in maximum dive depths across all diving events in 2011 ($F_{24} = 1.68$, $p = 0.21$) or in 2012 ($F_6 = 0.46$, $p = 0.65$). When examining mean dive depth across all dives, female rockhopper penguins dove deeper than female Magellanic penguins in 2011 ($F_{24} = 5.31$, $p = 0.01$), and deeper than both male and female Magellanic penguins in 2013 ($F_{20} = 10.17$, $p = 0.0007$; Table 3). There was no difference among the 3 species/sex groups in mean dive depth across all dives in 2012 ($F_6 = 0.53$, $p = 0.61$), though the data set was smaller for this year.

When examining only dives that contained wiggles, maximum dive depths obtained by individuals differed significantly between the 3 species/sex groups in both 2011 ($F_{24} = 4.00$, $p = 0.03$) and 2013 ($F_{20} = 8.15$, $p = 0.003$). In 2011 female rockhopper penguins performed deeper dives with wiggles than female Magellanic penguins, while in 2013 both female rockhopper and male Magellanic penguins performed deeper dives with wiggles than female Magellanic penguins (Table 3). Mean dive depth for dives with wiggles differed between species/sex groups in 2011 ($F_{24} = 3.26$, $p = 0.06$), but not in 2012 ($F_6 = 0.22$, $p = 0.81$) or 2013 ($F_{20} = 3.16$, $p = 0.06$). In 2011, female rockhopper penguins dove deeper than female Magellanic penguins, but not Magellanic male penguins (Table 3).

Stable isotope and niche analysis

Female rockhopper penguins differed from both male and female Magellanic penguins in their iso-

topic niche position (i.e. Euclidean distance) across all 3 years in our study (Table 4, Fig. 2). This difference was driven in part by the lower mean $\delta^{13}\text{C}$ values in female rockhopper penguins relative to both male (2011: Wilcoxon: $W = 0$, $p < 0.001$; 2012: $t = -5.88$, $p < 0.0001$; 2013: $t = -27.1$, $p < 0.0001$; Table 5) and female Magellanic penguins (2011: $W = 1$, $p < 0.0001$; 2012: $t = -6.36$, $p < 0.0001$; 2013: $t = -27.29$, $p < 0.0001$; Table 5). Female rockhopper penguins also had lower mean $\delta^{15}\text{N}$ values in all years relative to both male (2011: $t = -40.92$, $p < 0.001$; 2012: $W = 0$,

Table 4. Isotopic niche indices for female (F) rockhopper and male (M) and female Magellanic penguins during the breeding season, for the 3 years studied. Values represent pairwise differences (%) in isotopic niche position (Euclidean distance; lower left) and width (mean distance to centroid; upper right) between species/sex groups. ns: not significant; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$

Penguin species and sex	Rockhopper	Magellanic	Magellanic
	F	M	F
2011			
Rockhopper F	–	0.032 ^{ns}	0.18 ^{ns}
Magellanic M	7.9 ^{***}	–	0.22 ^{ns}
Magellanic F	7.6 ^{***}	0.99 ^{***}	–
2012			
Rockhopper F	–	0.47 ^{ns}	0.55 ^{ns}
Magellanic M	6.73 ^{***}	–	0.076 ^{ns}
Magellanic F	6.83 ^{***}	0.24 ^{ns}	–
2013			
Rockhopper F	–	0.47 ^{***}	0.43 ^{***}
Magellanic M	7.73 ^{***}	–	0.043 ^{ns}
Magellanic F	7.66 ^{***}	0.12 ^{ns}	–

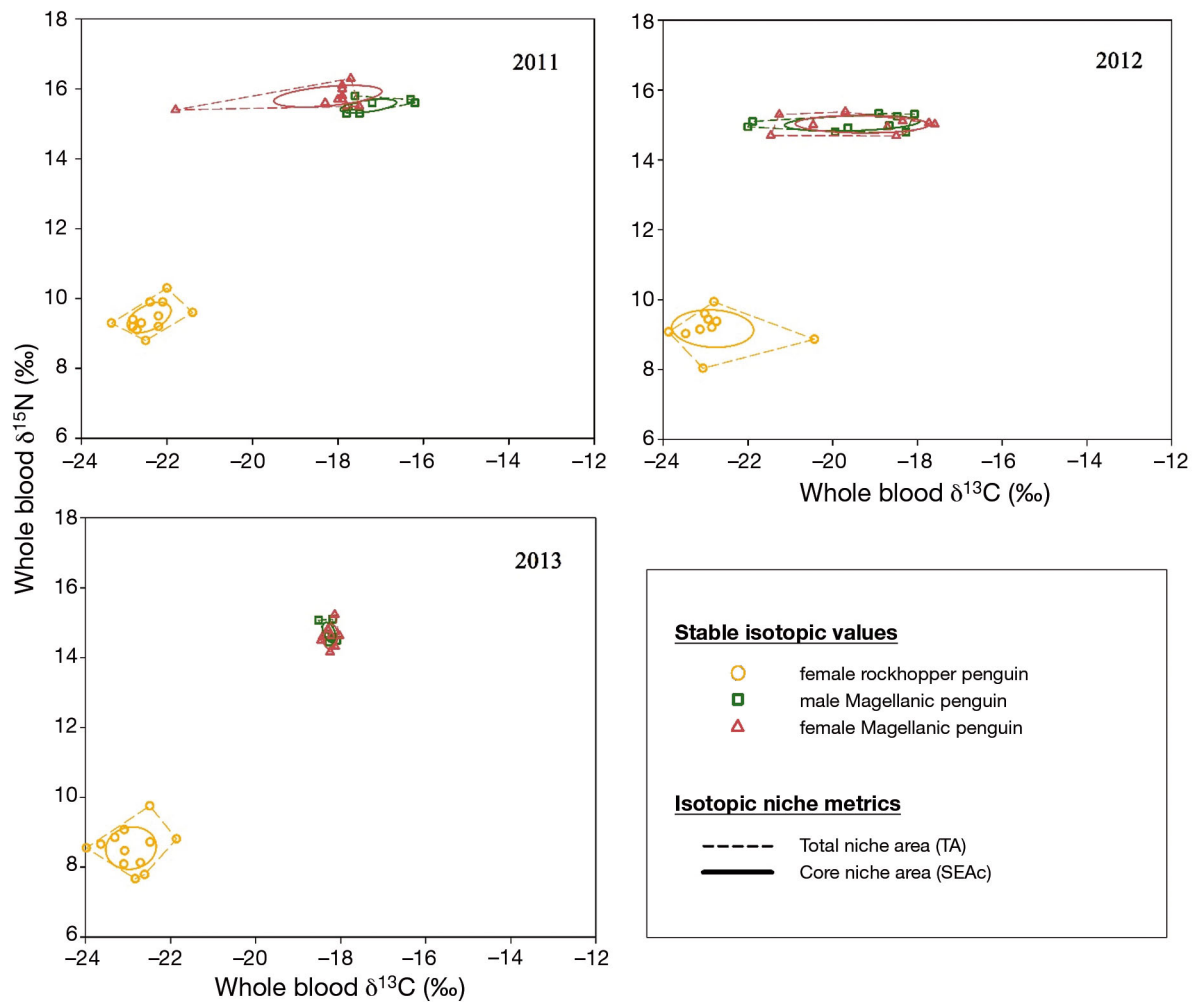


Fig. 2. Whole blood isotope values ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$), isotopic niche total and core areas of female rockhopper and male and female Magellanic penguins at Isla de los Estados, Tierra del Fuego, Argentina

$p = 0.0003$; 2013: $t = -26.42$, $p < 0.0001$; Table 5) and female Magellanic penguins (2011: $t = -42.01$, $p < 0.0001$; 2012: $W = 0$, $p < 0.0001$; 2013: $t = -26.79$, $p < 0.0001$; Table 5). In 2011 and 2012 the 3 species/sex groups had similar isotopic niche widths as measured by mean distance to centroid (MDC; Table 4). However in 2013, female rockhopper penguins had a significantly wider isotopic niche (Table 4), due to more variable $\delta^{13}\text{C}$ values relative to male (Bartlett's $k^2 = 9.2$, $df = 1$, $p = 0.002$) or female (Bartlett's $k^2 = 10.04$, $df = 1$, $p = 0.002$) Magellanic penguins. Core isotopic niche area (SEAc) and total niche

Table 5. Whole blood carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) stable isotope values for female (F) rockhopper and male (M) and female Magellanic penguins during the breeding season in each of the 3 years studied

Penguin species and sex	$\delta^{13}\text{C}$ (‰)		$\delta^{15}\text{N}$ (‰)	
	Mean \pm SD	Range	Mean \pm SD	Range
2011				
Rockhopper F	-22.4 ± 0.5	-23.3 to -21.4	9.5 ± 0.4	8.8 to 10.3
Magellanic M	-17.3 ± 0.6	-17.8 to -16.2	15.5 ± 0.2	15.3 to 15.8
Magellanic F	-18.2 ± 1.2	-21.8 to -17.5	15.8 ± 0.3	15.4 to 16.3
2012				
Rockhopper F	-22.8 ± 0.9	-23.9 to -20.4	9.2 ± 0.5	8.0 to 9.9
Magellanic M	-19.5 ± 1.5	-22.0 to -18.1	15.1 ± 0.2	14.8 to 15.3
Magellanic F	-19.3 ± 1.5	-21.5 to -17.6	15.0 ± 0.2	14.7 to 15.4
2013				
Rockhopper F	-22.9 ± 0.6	-24.0 to -21.9	8.6 ± 0.6	7.7 to 9.8
Magellanic M	-18.3 ± 0.1	-18.5 to -18.1	14.7 ± 0.3	14.5 to 15.1
Magellanic F	-18.3 ± 0.2	-18.5 to -18.0	14.6 ± 0.3	14.2 to 15.2

areas (TA) of female rockhopper penguins did not overlap with either male or female Magellanic penguins in any of the 3 years of our study (Fig. 2). At the individual level, no female rockhopper penguin isotopic values were encompassed by the TA of either male or female Magellanic penguins in any of the 3 years of our study (Fig. 2).

Niche position between male and female Magellanic penguins only differed in one (2011) of the 3 years of our study (Table 5, Fig. 2). Differences in 2011 were driven by lower mean $\delta^{13}\text{C}$ values ($W = 90.5$, $p = 0.002$) in females relative to males. $\delta^{15}\text{N}$ values also statistically differed between sexes in 2011 ($t = -2.48$, $p = 0.023$), but the mean difference was within the level of our analytical precision (0.2‰) and thus is biologically insignificant. MDC did not differ between sexes in Magellanic penguins in any of the years of our study (Table 5, Fig. 2). SEAc overlapped greatly between male and female Magellanic penguins in 2012 (80–92%) and 2013 (62–86%), but did not overlap in 2011 (Fig. 2). Overlap in TA was similar, with high overlap in 2012 (63–84%) and 2013 (52–63%) but none in 2011 (Fig. 2). However, individuals of both sexes were encompassed within the TA of the opposite sex in all years (Fig. 2). Isotopic niche overlap at the individual level ranged from 9 to 33% in 2011, 33 to 44% in 2012 and 25 to 86% in 2013.

DISCUSSION

We found a consistent pattern of foraging niche segregation between sympatric rockhopper and Magellanic penguins on Isla de los Estados across the 3 breeding seasons examined. Direct tracking indicated spatial foraging niche segregation between species in both foraging areas (horizontal axes) and diving depths (vertical axes). We also observed clear differences in the isotopic niches of species indicative of lower trophic position ($\delta^{15}\text{N}$) and greater use of offshore foraging habitats ($\delta^{13}\text{C}$) by female rockhopper penguins relative to male and female Magellanic penguins. In contrast, there was little evidence of intra-specific foraging niche segregation between male and female Magellanic penguins.

Inter-specific foraging niche segregation

Ecological niche theory predicts that sympatric species should segregate their niches along one or more axes in order to reduce competition (Hutchin-

son 1957). In agreement with this theory, we found a consistent pattern of spatial and trophic foraging niche segregation between sympatric rockhopper and Magellanic penguins on Isla de los Estados.

Kernel density distributions derived from direct tracking data indicated strong spatial segregation of foraging locations between female rockhoppers and male/female Magellanic penguins. In general there was little overlap between species foraging areas ($\leq 35\%$) and only female rockhopper penguins explored areas further south and offshore from the shelf break. When spatial overlap occurred it was due to a few female rockhopper penguins foraging in areas northwest from Isla de los Estados, and a few male and female Magellanic penguins foraging in areas southeast from Isla de los Estados. These findings agree with the only other past study to examine the foraging ranges of these species in sympatry. Masello et al. (2010) found that the foraging areas of rockhopper and Magellanic penguins overlapped very little (5%) during a single breeding season on the Falkland/Malvinas Islands.

In addition, our findings agree with a previous study using time–depth recorder data at Isla de los Estados, which found that female rockhopper penguins foraged in shelf waters or in the more pelagic waters off the shelf-break (Schiavini & Raya Rey 2004). While no other tracking studies have taken place at Isla de los Estados, Magellanic penguins breeding at other colonies are also known to forage relatively close to the colony during the breeding season (Radl & Culik 1999, Raya Rey et al. 2012b). Then, the foraging distances of both species obtained in this study are consistent with those found in previous studies. The fact that there were no differences in maximum foraging distances between species is also in line with the constraints of central-place foraging, and the fact that during the early chick rearing period foraging distance may affect the reproductive success of the penguins (Boersma & Rebstock 2009).

Spatial segregation was also apparent in species diving behavior. Female rockhopper penguins dove consistently deeper than female Magellanic penguins, and often dove to the same depths or deeper than male Magellanic penguins. Diving depths of female rockhopper penguins in this study were consistent with those found by other studies in the region (Schiavini & Raya Rey 2004). However, differences in diving depths between species were not associated with differences in body size. While larger seabirds are usually able to dive deeper than smaller seabirds (Wilson 2010, Ratcliffe et al. 2014), Magellanic pen-

guins are larger than rockhopper penguins (Gandini et al. 1992, Hull 1996). Instead, the differences in dive depths explored by penguins in this study were likely associated with the Magellanic penguins performing dives in more near-shore areas and the relatively deeper-diving rockhopper penguins foraging in pelagic and mesopelagic zones farther offshore, as observed from tracking and $\delta^{13}\text{C}$ isotope results. In addition, the differences in depths of the water column explored by the penguins in this study are likely to be related to diet composition, as different type of prey or even different sizes of prey may be found in the water column (Wilson 2010).

In each of the 3 seasons examined, female rockhopper penguins breeding on Isla de los Estados differed in their isotopic niche relative to male and female Magellanic penguins during the early chick rearing period. Isotopic niche partitioning between species was due to lower trophic position (e.g. lower $\delta^{15}\text{N}$ values) and greater use of offshore/pelagic waters (e.g. lower $\delta^{13}\text{C}$ values) by rockhopper penguins relative to Magellanic penguins. Trophic segregation was quite strong (~5‰ difference in $\delta^{15}\text{N}$ values) between penguin species and was consistent throughout all years examined. As $\delta^{15}\text{N}$ values usually increase by 3 to 5‰ per trophic level in marine food webs (Post 2002), this likely indicates a full trophic level difference in the diet of rockhopper and Magellanic penguins during the breeding season at Isla de los Estados. These results agree with prior conventional dietary studies that indicate during the chick rearing period rockhopper penguin diets are dominated by euphausiids and hyperiid amphipods (such as *Themisto gaudichaudii*) and, to a lesser extent, juvenile cephalopods and larval and juvenile fishes (Raya Rey & Schiavini 2005). In comparison, the diet of Magellanic penguins at other colonies in Southern Patagonia (Argentina and Chile) indicate that they prey mostly on spratt *Sprattus fuegensis* and squat lobster *Munida gregaria* and, to a lesser extent, on cephalopods (e.g. *Loligo gahi*) (Frere et al. 1996, Radl & Culik 1999, Scioscia et al. 2014). Stable isotope data provided additional support for differences in foraging habitats between species. In this study, $\delta^{13}\text{C}$ values were always lower for female Rockhopper penguins compared to male and female Magellanic penguins. Combining tracking and diving data, our results strongly indicate a general pattern of habitat niche segregation, given that female rockhopper penguins were likely to dive deeper and travel further offshore, off the shelf break during their foraging trips. This agrees with past studies indicating female rockhopper penguins often feed on

mesopelagic prey (Schiavini & Raya Rey 2004, Raya Rey & Schiavini 2005) associated with marine fronts such as the Antarctic Circumpolar and the Falkland/Malvinas currents (Schiavini & Raya Rey 2004).

Studies on food consumption by rockhopper and Magellanic penguins at other breeding colonies suggest that Magellanic penguins have a greater impact on the ecosystem than rockhopper penguins in terms of the amount of prey consumed per day (Brown 1989, Sala et al. 2012). Even so, due to their larger numbers, breeding rockhopper penguins at Isla de los Estados have a greater potential to exert competitive pressure on the smaller number of breeding Magellanic penguins, relative to the opposite. The few available studies indicate that the study area is productive in terms of the biodiversity and abundance of prey resources, including zooplankton, fish and cephalopods (Sanchez et al. 1995, Hansen 1999, Ivanovic 2010, Padovani et al. 2012), with high concentration of zooplankton south of 45° (Sabatini & Colombo 2001, Sabatini et al. 2004, Romero et al. 2006) in line with the Patagonian Cold Estuarine Front (Acha et al. 2004). However, no concurrent data is available to assess how variability in the abundance of prey resources in the study area influenced the foraging ecology of the 2 penguin species or the potential for competition during our study years.

While this study focuses on foraging niche segregation in 2 penguin species, there are also other potential competitors in the study region. Species of large fish, such as longtail hake *Macrurus magellanicus*, other seabirds such as cormorants, albatrosses and petrels, and also marine mammals, such as dolphins and sea lions, have been registered in the study area and some also breed on Isla de los Estados (Schiavini & Raya Rey 2001, Falabella et al. 2009, Copello et al. 2011, Padovani et al. 2012 and references therein). While these species also likely act as large consumers of pelagic zooplankton, fish and cephalopods, relatively less is known about their diets and foraging distribution in the study area (e.g. *Lagenorhynchus australis*; Schiavini et al. 1997). Further studies on the larger food web in this region would help to better understand the interaction within and between different species inhabiting the ecosystem.

Intra-specific niche segregation

The intensity of intra-specific competition within central-place foragers is thought to be directly re-

lated to the density of individuals and/or the availability of prey resources within an area (Cairns 1989). Methods to avoid intra-specific competition include partial or complete spatial partitioning of horizontal or vertical foraging areas either among sexes or between individuals from nearby breeding colonies (Masello et al. 2010, Raya Rey et al. 2013), or even between individuals of different ages (young and adults; Forero et al. 2002, 2005, Michalik et al. 2013). However, in our study, male and female Magellanic penguins exhibited a strong overlap in foraging areas in all 3 years examined at Isla de los Estados. Nor did Magellanic penguins present sexual differences in the maximum distances from the colony reached during foraging trips. Maximum distance from the colony for the species were similar to those observed at other colonies of this species (Radl & Culik 1999, Raya Rey et al. 2010). Magellanic penguins breeding in Martillo Island, the nearest colony of the species to our study area, also presented no differences in the distance of male and female Magellanic penguin trips (Raya Rey et al. 2010).

We also found little evidence that male and female Magellanic penguins in our study consistently partitioned their respective vertical foraging areas during the early chick rearing period. In 2011 and 2012 both sexes dove at similar depths, while in 2013 male Magellanic penguins on average dove deeper than female Magellanic penguins. Some sexual differences in diving behaviors might be expected due to body size alone, with larger males being able to dive deeper than smaller females (Walker & Boersma 2003, Raya Rey et al. 2012b). For example sexual differences in dive depths among Magellanic penguins have been observed during the incubation period in a past study (Raya Rey et al. 2012b).

Stable isotope analyses have been used successfully in previous studies to identify sex-specific trophic and/or foraging habitat niche segregation in seabirds (e.g. Raya Rey et al. 2012a). However, similar to both tracking and diving data, we saw little evidence of isotopic niche partitioning between male and female Magellanic penguins at Isla de los Estados. Niche position between male and female Magellanic penguins only differed in one of the 3 years of our study and were due to lower mean $\delta^{13}\text{C}$ values in females relative to males. Even so, isotopic niche width did not differ between sexes in any years, and individuals of both sexes were encompassed within the isotopic niche area of the opposite sex in all years. These results indicate few differences in the trophic level of diets and foraging habitats used by male and female Magellanic penguins breeding in Isla de los

Estados. However, one past study of the diet of Magellanic penguins breeding in Northern Patagonia (Argentina) indicated that males consume a greater proportion of fish (anchovy) than females (Forero et al. 2002). Even so, male and female Magellanic penguins breeding on Martillo Island, the nearest colony of this species in Southern Patagonia (Argentina) have similar diets, with no evident sexual segregation in prey selection (Scioscia et al. 2014). While examining inter-annual variation within species foraging ecology was not a primary focus in this study, it is interesting to note the difference in isotopic niche area of Magellanic penguins in 2013 relative to 2011 and 2012. In 2013, both male and female Magellanic penguins had quite small core and total isotopic niche areas due to population level $\delta^{13}\text{C}$ values that were much less variable relative to other years. However, the narrower isotopic niche observed in 2013 did not appear to be correlated with similar inter-annual variation in horizontal or vertical foraging axes from direct tracking and diving data. While it is difficult to estimate the cause for the narrower isotopic niche of Magellanic penguins in 2013, one possible explanation might be specialization on a particular prey resource and/or microhabitat. Interestingly, this observed narrower isotopic niche did not appear to negatively affect the breeding success of Magellanic penguins in 2013 (1.85 chicks per nest) relative to 2011 (1.88 chicks per nest) or 2012 (2 chicks per nest) as measured by nests of penguins equipped with loggers (N. Rosciano unpubl. data).

CONCLUSIONS

We assessed foraging niche segregation within and between 2 central-place foraging penguin species breeding on Isla de los Estados. These sympatric species exhibited constant differences along trophic and foraging habitat niche axes that helped to differentiate the niches from one another. Direct tracking, diving and isotopic data indicated a lower trophic position and greater use of offshore foraging habitats by female rockhopper penguins relative to Magellanic penguins that preferentially used coastal waters and fed at a higher trophic level. These differences likely act to reduce competition between the 2 species during the breeding season when they are constrained to exploit resources within a given range around their colonies.

In contrast, we found little evidence to suggest intra-specific segregation between the foraging niches of male and female Magellanic penguins

breeding in Isla de los Estados. This is unexpected as sexual dimorphism in body size and evidence from studies at other breeding sites indicate the potential for differences in diving depths and diets between sexes (Forero et al. 2002, Raya Rey et al. 2012b), and the potential for intra-specific competition is often higher than competition among congeners (Masello et al. 2010, Raya Rey et al. 2013). Possible explanations for the lack of sex-specific foraging niche segregation of Magellanic penguins at Isla de los Estados may be related to their relatively small population size (e.g. density dependence; Schiavini et al. 2005, Raya Rey et al. 2014) and/or the availability of prey resources within the area (e.g. resource availability; Sanchez et al. 1995, Hansen 1999, Acha et al. 2004). In addition, as a previous study in the Malvinas/Falkland Islands reported foraging niche segregation between neighboring populations of Magellanic penguins, it may be that intra-specific competition between populations is stronger than within populations (Masello et al. 2010).

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