Marine Biology (2023) 170:96
https://doi.org/10.1007/s00227-023-04242-z

ORIGINAL PAPER

Variation in the trophic niche and food provisioning between the early and late chick-rearing stages in Magellanic penguins *Spheniscus magellanicus* at Martillo Island, Tierra del Fuego, Argentina

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Received: 24 January 2023 / Accepted: 1 June 2023 / Published online: 20 June 2023

Abstract

Variation in the foraging niche and parental provisioning behaviors of breeding seabirds have the potential to affect population dynamics (e.g. foraging success, breeding productivity, and ultimately population size). We sampled blood plasma of family' groups (females, males, and chicks) of Magellanic penguins (*Spheniscus magellanicus*) from Martillo Island, Argentina. We used stable isotope analyses on plasma samples to examine food provisioning, isotopic niche, trophic position, and diet composition of penguins between the early and late chick-rearing periods. We found clear differences in the isotopic niches of penguins between the two stages of the chick-rearing period related to shifts in foraging habitat and/or diet composition between stages. We found no evidence of individual consistency in isotopic niches or sex-specific selective provisioning by adults. In addition, we found high variability within family groups (accounting for 90% of the total isotopic variability). This study improves our understanding of the age, sex, individual, and breeding stage-specific trophic niches of Magellanic penguins, which may be helpful in projecting how they may respond to future environmental change (e.g., changes that affect prey availability).

Keywords Food provisioning · Stable isotopes · Breeding season · Seabirds

Introduction

Understanding differences in resource partitioning between organisms is central to ecology. Optimal foraging theory has long been used to understand and predict prey choice and patch use in animal populations (Stephens and Krebs 1986). One of the key predictions of this theory is that variation in prey choices is driven by intraspecific competition which is expected to increase both population and individual niche breadth (Araújo et al. 2008).

In this context, the foraging behavior of seabirds is affected by the distribution and abundance of prey such that inter-annual and seasonal variation in resource availability can influence their foraging strategies and fitness (Watanuki 1992; Votier et al. 2008; Sanz-Aguilar et al. 2009). In addition, seabirds also exhibit intra-specific variation in foraging strategies due to factors such as sex, age, morphology, breeding status, and individual specialization (Bolnick et al. 2003; Raya Rey et al. 2012b; Le Vaillant et al. 2013; Ceia and Ramos 2015). Quantifying the degree of temporal and intra-specific variation of foraging niches and identifying their drivers is relevant, as they have the potential to affect foraging and breeding success, and ultimately population trends (Lynch et al. 2012; Waluda et al. 2012; Horswill et al. 2017).

Colonial seabirds, such as penguins, are central place foragers (Orians and Pearson 1979), and therefore are easily accessible when breeding. During this period, they are

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Responsible Editor: V. Paiva.

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obliged to capture enough food to provision their chicks and themselves (Croxall and Davis 1999; Boersma et al. 2015). This tradeoff may preference chicks, with adults provisioning chicks with higher quality food items in respect to those they consume for themselves (Forero et al. 2002; Dehnhard et al. 2016). Alternatively, adults may favor self-provisioning and prioritize survival over reproductive success (Ballard et al. 2010; Booth and McQuaid 2013). This balance could also be influenced by sexual differences in the foraging behaviors that are driven by morphological differences between parents (Rosciano et al. 2019).

In sexually dimorphic and diving species, the body size is allometrically correlated with diving capacities (i.e., larger-bodied individuals can dive deeper) (Noren et al. 2001). In turn, this could affect the amount and type of food provided by parents of different sexes. In penguins, past studies have examined differential investment in food provisioning by parents. Adelie penguin (*Pygoscelis adeliae*) females made on average longer foraging trips than males, resulting in a lower provisioning rate compared to males (Clarke et al. 1998). Meanwhile, Macaroni penguins (*Eudyptes chrysolophus*) females provision their chicks throughout the rearing period and at higher rates than males, which only participate in later stages (Barlow and Croxall 2002). Similarly, southern rockhopper penguins (*Eudyptes chrysocome*) females provide most of the food during chick rearing and they feed their chicks with higher trophic level prey than they consume for themselves (Rosciano et al. 2019). Magellanic penguins from North Patagonia have selective food provisioning since chicks have a more similar diet to their male parent and this pattern was more evident at colonies and seasons where penguins had a more diverse diet (Ciancio et al. 2018).

Magellanic penguins (*Spheniscus magellanicus*) are moderately sexually dimorphic, males have a larger size and are heavier than females (Boersma et al. 2013) and are opportunistic and pelagic foragers, depending on the season and prey species abundance and availability in the region (Scolaro et al. 1999; Clausen and Pütz 2002; Scioscia et al. 2014; Dodino et al. 2020). Magellanic penguins typically lay two eggs, and hatching success could be variable among colonies and years (Boersma et al. 2013). Brood reduction takes place after hatching, and the larger of the two chicks, usually the first hatchling, receives more food (Blanco et al. 1996; Boersma et al. 2013). Tierra del Fuego colonies represent the southernmost breeding range and their individuals are known to feed on key regulatory species of the food web in the Beagle Channel (e.g. *Grimothea gregaria*, *Sprattus fuegensis*) (Scioscia et al. 2014; Diez et al. 2016, 2018; Dodino et al. 2020). Particularly, the pelagic aggregations of both species, *G. gregaria* and *S. fuegensis*, occur all year throughout the channel but during winter the latter increases its availability in the inner sector of the channel (Diez et al. 2018). In addition, an expansion in the distribution and abundance of pelagic swarms of *G. gregaria* was reported for the Beagle Channel in recent years (Diez et al. 2016).

In Martillo Island, the diet and foraging ecology of breeding Magellanic penguins have been studied in terms of the type of food, using stomach content methodology (Scioscia et al. 2014), in terms of their isotopic niche during early chick-rearing (Dodino et al. 2022) and the diving behavior using time and depth recorders and GPS-TD loggers during early chick-rearing (Raya Rey et al. 2010, 2012a; Harris et al. 2020). All these studies have reported different degrees of variability in the feeding ecology of the species related to their generalist habitat. For example, (Scioscia et al. 2014) reported variability in the diet composition among different reproductive stages and years, and suggest a potential relationship with changes in the distribution and abundance of their main prey. While Raya Rey et al. (2012a) reported sex-related differences in diving foraging behavior and suggested that those differences could be related to changes in *S. fuegensis*' availability. However, those studies have not explored potential differences in self-provisioning and chick-provisioning behaviors.

Stable isotope analyses (SIA) of carbon (δ^{13}C) and nitrogen (δ^{15}N) provide the ability to assess animals' diet and habitat use over both short and longer-term time scales (Inger and Bearhop 2008; Layman et al. 2012; Cherel et al. 2014). δ^{13}C and δ^{15}N values act as measures of the scenopoetic (i.e. habitat) and bionomic (e.g. diet) components of a consumer's trophic niche, referred to as the "isotopic niche" (Newsome et al. 2007). The isotopic niche framework is a useful tool to assess foraging habitat and diet shifts between stages of species' annual cycle. Blood plasma in penguins integrates dietary information over an approximately 15-day period (Barquete et al. 2013; Jenkins et al. 2019). As such, blood plasma collected during the middle of the early and late chick-rearing stages, which each have a duration of approximately 30 days in Magellanic penguins (Boersma et al. 2013), would facilitate isotopic niche comparisons between these two stages. Moreover, collecting plasma samples from adults of both sexes and their chicks provides a robust methodology to analyze parental-provisioning, sex-specific, and individual-based strategies across the early and late chick-rearing stages.

In this context, the main objective of this study was to evaluate temporal, individual, and sex-specific variation in the trophic niche and food provisioning of Magellanic penguins between early and late chick-rearing stages (ECR and LCR, respectively), at Martillo Island, Beagle Channel, Argentina, using stable isotope analysis of blood plasma. We defined "seasonal consistency" as reflecting population-level metrics of penguin diets (i.e., isotopic niche, trophic position, diet composition) that remain consistent between the two stages. In contrast, we define "individual consistency" as intra-individual differences in diets that remain consistent between stages (i.e., same values of stable isotopes) even if there is an overall shift in diet at the population level (e.g., Herman et al. 2017). In addition, we defined "selective provisioning" as when one adult sex (male or female) selectively feeds the chicks more than the other adult (e.g., Rosciano et al. 2019). Taking into account these definitions, we hypothesized that (1) at the population level, the isotopic niches of adults and the chicks they provision will differ between ECR and LCR stages reflecting seasonal shifts in diet composition and/or foraging habit use between these two stages, (2) inter-individual differences in diets will be inconsistent between stages similar to Rosciano et al. (2020) reflecting a lack of individual consistency, (3) breeding adults have sex-specific selective provisioning based on previous studies on the species (Ciancio et al. 2018) and as a consequence of differences in prey selection between parents.

Methods

Study area and sample collection

We conducted fieldwork at the Magellanic penguin colony on Martillo Island (54° 54′ S, 67° 23′ W). This hammer-shaped island is located in the eastern section of the Beagle Channel (Tierra del Fuego, Argentina) and holds ca. 4900 active nests (Raya Rey unpubl. data). We sampled 13 family groups during the ECR (chicks with 30 days old, late-November to early-December 2016) and during the LCR (chicks with 60 days old, mid-January 2017). We collected samples from 13 females, 13 males and 21 chicks in each stage, totalling 94 samples. All the nests had two chicks at the beginning of the season, but five chicks died before the late-chick rearing stage, consequently, the early samples of those chicks were not considered. In each breeding stage, we collected 3 ml of whole-blood from the tarsal vein for each member of the family group (female, male and chicks). Adults' sex determination was based on differences in beak widths and lengths (Gandini et al. 1992). Chicks were identified by making a small cut in the interdigital webbing to one of them. Each blood sample was centrifuged in the laboratory (1000 rpm, 30 min) on the same day it was collected to separate the plasma from the blood cells. Each fraction was preserved in hermetic tubes at − 80 °C until further carbon and nitrogen isotope processing in the laboratory (Hobson et al. 1997).

Stable isotope analysis

We lyophilized plasma samples for 12 h then homogenized and weighed samples (0.6 mg ± 0.1 mg) and into tin cups. Sample was flash-combusted (Costech ECS 4010 elemental analyzers) and analyzed for carbon ($\delta^{13}C$), nitrogen ($\delta^{15}N$) stable isotope values, and C:N ratios via an interfaced Thermo Scientific Delta XP continuous-flow stable isotope ratio mass spectrometer at Louisiana State University. USGS 40 and USGS 41 glutamic acid reference materials were used to normalize sample values. Sample precision based on the repeated sample and reference material was 0.1‰ for both $\delta^{13}C$ and $\delta^{15}N$ values. Stable isotope values are expressed in δ notation in per mil units (‰), according to the following equation:

$$\delta X = \left[\left(R_{sample}/R_{standard}\right) - 1\right]$$

where X represents either ^{13}C and ^{15}N and R the ratio between $^{15}N/^{14}N$ or $^{13}C/^{12}C$. $R_{standard}$ for $\delta^{15}N$ was based on atmospheric N_2 while for $\delta^{13}C$ was based on Vienna Pee Dee Belemnite (V-PDB). Average plasma C:N values ranged from 3.58 to 5.11 (Table 1) indicating variable lipid content among samples (Post et al. 2007). Therefore, prior to statistical analysis, we normalized plasma $\delta^{13}C$ values using the equation of Post et al. (2007) for aquatic organisms:

$$\delta^{13}C_{normalized} = \delta^{13}C_{untreated} - 3.32 + 0.99 * C : N$$

Table 1 Carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) stable isotope values of plasma samples after linear mixed model analysis for each sex/age (adult female, adult male, chicks) and stage (ECR: early-chicks rearing; LCR: late-chicks rearing). Values presented are mean ± SD and the percentage (%) of variability between and within family groups for each model. Different letters indicate significant differences between sex/stages after Tukey's HSD post-hoc test ($p < 0.05$)

Sex/stage	$\delta^{13}C_{normalized}$			$\delta^{15}N$			$C_{raw}:N$
	Mean ± SD	% between	% within	Mean ± SD	% between	% within	
Female, ECR	-16.4 ± 0.2^{a}	28.5	71.5	15.6 ± 0.2^{a}	19.0	81.0	3.98
Male, ECR	-17.1 ± 0.2^{a}			$15.4 \pm 0.2^{a,c}$			3.93
Chick, ERC	-17.1 ± 0.1^{a}			15.4 ± 0.1^{a}			5.11
Female, LRC	-17.8 ± 0.2^{b}			$15.1 \pm 0.2^{b,d}$			4.10
Male, LRC	-17.9 ± 0.2^{b}			$15.3 \pm 0.2^{b,c}$			4.07
Chick, LRC	-18.0 ± 0.1^{b}			15.0 ± 0.2^{d}			3.58

Isotopic niche analysis and consistency at population level

At population level, we used plasma $\delta^{13}C$ and $\delta^{15}N$ values to characterize isotopic niche overlap and differences in isotopic niche area among adults and their chicks as a *proxy* of the trophic niche overlap and size (Newsome et al. 2007). Specifically, we calculated standardized ellipse areas (SEA) corrected for small sample sizes (SEA_C) for adult females, adult males, and chicks separately for each breeding state (i.e. ECR and LCR) and between sexes/ages within each stage (Jackson et al. 2011). We estimated isotopic niche overlap as the proportion of SEA_C for each group that overlaps with a comparison group's SEA_C. In addition, we constructed Bayesian SEAs (SEA_B) using the Stable Isotopes Bayesian Ellipses (SIBER, Jackson et al. 2011) package in R version 3.4.0 (R Core Team 2021) to compare two-dimensional isotopic niche areas among groups. We then used the resulting Bayesian posterior probability distributions of SEA_B to calculate the pairwise probabilities that isotopic niche areas from one group are different than a comparison group (Jackson et al. 2011).

We examined consistencies between stages using a generalized lineal model (GLM) with Gaussian distribution (nlme package, Pinheiro et al. 2015) where the response variable was the $\delta^{15}N$ and $\delta^{13}C$ values for each sex/age group and the explanatory variable was the stage (ECR and LCR) (6 models totally).

Trophic position estimates (population level)

We estimated the trophic position (TP) of adult females, adult males, and chicks separately for each breeding state (ECR and LCR) using the Bayesian approach of the *tRophicPosition* package in R (version 4.0.3, Quezada-Romegialli et al. 2018). We selected the *jagsOneBaseline* model and we selected as baseline the values of mussels previously reported at Martillo Island ($\delta^{13}C = -17.1 \pm 0.4$ ‰, $\delta^{15}N = 12.2 \pm 0.3$ ‰; Dodino et al. 2020). We assumed mussels incorporate the isotopic signal of the entire water column and were completely herbivorous and occupied a TP of 2. We used the trophic discrimination factor (TDF) of 2.6 ± 0.5 ‰ for $\delta^{15}N$ values estimated for plasma tissue from Magellanic penguins (Jenkins et al. 2019). We evaluated differences in TP between sex/age groups using the *compareTwoDistributions* function (Quezada-Romegialli et al. 2018).

Mixing model analyses (population level)

We used a Bayesian stable isotope mixing model to compare the diet composition of the sexes/ages between stages ('MixSiar' in R, Stock et al. 2018). Taking into account previous information on adults Magellanic penguins' diet (Schiavini et al. 2005; Scioscia et al. 2014; Dodino et al. 2020) and their foraging areas during the ECR stage i.e., close to the colony, within the Beagle Channel (Raya Rey et al. 2010; Harris et al. 2020), and during the LCR stage, i.e. eastward feeding areas, near to Picton Island (55° 4.5′ S 66° 53.3′ W) (Raya Rey unpubl. data), we selected published stable isotope data of potential prey items collected along the Beagle Channel (e.g., the squat lobster *Grimothea gregaria*, the Fuegian sprat *Sprattus fuegensis*) (Riccialdelli et al. 2020).

Following the approach of Dodino et al. (2020), we combined prey species into three statistically and ecologically relevant prey groups based on their TPs estimated in previous works to reduce model uncertainty and to aid in interpretation: (1) low-trophic level species (TP ~ 2): pelagic form of the squat lobster *G. gregaria* (2) mid-trophic level species (TP ~ 3) with a mix of small pelagic, bentho-pelagic species such as the benthic form of *G. gregaria*, fuegian sprat *S. fuegensis*, and notothenioid *Patagonotothen tessellata* and *P. ramsayi*, (3) mid-trophic level species (TP ~ 3–4) with coastal species such as *Eleginops maclovinus, P. cornucola*, and *Odontesthes smitti* (Table S1).

Given the fact that the years in which prey group stable isotope values were available did not fully coincide with the year in which penguin plasma were collected, the use of these prey values has the potential to add uncertainty to our model predictions. For this reason, we applied the same correction factor used by Riccialdelli et al. (2020) in all $\delta^{13}C$ values of prey items and penguin samples to account for the Suess effect (Francey et al. 1999; Indermühle et al. 1999) and to further reduce the potential for temporal biases in mixing model results. We modeled the contribution of each food source to the synthesis of Magellanic penguin blood using the TDF of − 0.6 ± 0.5 ‰ for $\delta^{13}C$ and 2.6 ± 0.5 ‰ for $\delta^{15}N$ (Jenkins et al. 2019). We ran the model over 3 Markov Chain Monte Carlo chains of 3,000,000 iterations and discarded the first 1,500,000 (Gelman and Rubin 1992). We used a prior of 25% for group 1, 25% for group 2, and 3% for group 3. The prior was selected based on previous information on diet composition data for Magellanic penguins (Scioscia et al. 2014; Dodino et al. 2020).

Individual consistency

To test whether individual diets and foraging habitats are consistent between stages, we tested for relationships between individual's ECR and LCR $\delta^{15}N$ and $\delta^{13}C$ values using Pearson correlations for normally distributed population.

Family groups

We evaluated differences in δ^{13}C and δ^{15}N values between members of the family groups (females, males, and chicks), using generalized linear mixed effect models (GLMMs). We used one model for each response variable (δ^{13}C, δ^{15}N), the explanatory variables were sex/age group and the chick-rearing stage, and the random factor was the family identity to take into account the variability within family groups. We provided the estimate, the standard errors (SE), the *t* value, the *p* value, and the confidence interval (CI) for each model. Then, we conducted a posteriori Tukey HSD test for multiple comparisons (multicomp package; Hothorn et al. 2008).

To evaluate a possible relationship between chicks' stable isotope values (δ^{13}C, δ^{15}N) and their parents' stable isotope values, we ran GLM with Gaussian distribution using chick's stable isotope values as a response variable and parents' stable isotope values as an explanatory variable. A separate model was made by stage for each isotope, that is, a total of eight models.

Finally, we chose the heuristic Euclidean distances (ED) (Phillips 2001) between chicks and parent as a *proxy* of diet similarity. This is given by:

$$ED = \sqrt{\left[\left(\delta 13\mathrm{C}_{\mathrm{chick}} - \delta 13\mathrm{C}_{\mathrm{adult}}\right)2 + \left(\delta 15\mathrm{N}_{\mathrm{chic}}\mathrm{k} - \delta 15\mathrm{N}_{\mathrm{adult}}\right)2\right]}$$

where ED is the isotopic Euclidean distance and the other terms are the isotope values for chick and adults, respectively. If we assume that if parents have different stable isotope values due to individual or sex-specific differences in diet, chick's stable isotope values will be most similar to the individual parent that provisions them with the most food (i.e., have the smallest ED between parent and chick). To evaluate the effect of adult' sex on ED, we run GLMMs with gamma distribution and log link function using the ED as a response variable, sex as an explanatory variable, and family identity as a random variable.

Results

Seasonal and isotopic niche consistency (population level)

Females, males, and chicks did not overlap their isotopic niches between the two chick-rearing stages (0% overlap in all comparisons, Fig. 1). In contrast, within each stage, we found a large degree of niche overlap among sexes/ages (Fig. 2). During the ECR females-males overlap' corresponded to 58% and 65% of their isotopic niches, respectively (Fig. 2). Between females and chicks, the overlap represented 73% and 92% of their isotopic niches, respectively (Fig. 2). Moreover, the overlap between males-chicks represented 52% and 60% of their isotopic niches, respectively (Fig. 2). During the LCR females-males overlap', corresponding to 25% and 43% of their isotopic niches, respectively (Fig. 2). Between females-chicks, the overlap corresponded to a 43% and 54% of their isotopic niches, respectively (Fig. 2). Males-chicks overlap', corresponding to 56% and 40% of their isotopic niches, respectively (Fig. 2).

SEA$_B$ predicted different niche widths between ages/stages (Fig. 3). Between stages, the three sexes/ages showed the largest isotopic niche during the ECR than the LCR (Pairwise-probabilities, females-ECR > females-LCR: 95%, males-ECR > males-LCR: 70%, chicks-ECR > chicks-LCR: 75%). During the ECR, females showed the largest isotopic niche and the males the narrowest (Pairwise-probabilities, females > males: 63%; females > chicks: 77%, chicks > males: 65%). During the LCR females, again, showed the largest isotopic niche, but now, the chicks showed the narrowest (Pairwise-probabilities, females > males: 78%; females > chicks: 94%, males > chicks: 79%).

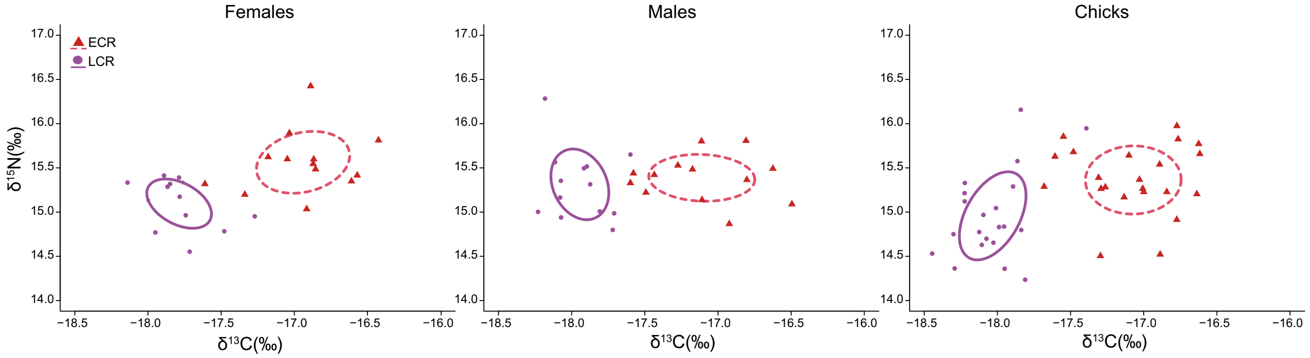

Fig. 1 Standard ellipses corrected for small sample size (SEA$_C$) estimated from δ^{13}C and δ^{15}N values of plasma samples collected from Magellanic penguins of Martillo Island during the chick-rearing period (*ECR* early-chicks rearing in red, *LCR* late-chicks rearing in purple) and grouped by sex/age (females, males, chicks)

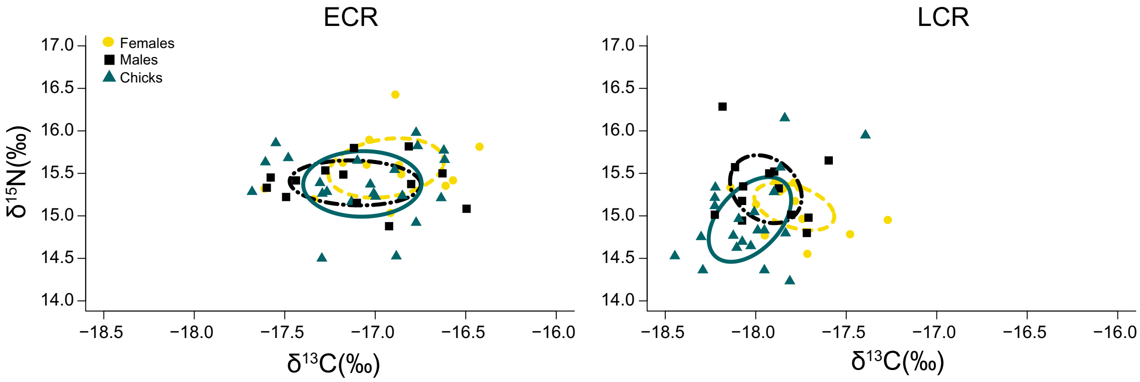

Fig. 2 Standard ellipses corrected for small sample size (SEA_C) estimated based on $\delta^{13}C$ and $\delta^{15}N$ values of plasma samples collected from females, males, and chicks of Magellanic penguins sampled in Martillo Island grouped by chick-rearing period (*ECR* early-chicks rearing, *LCR* late-chicks rearing)

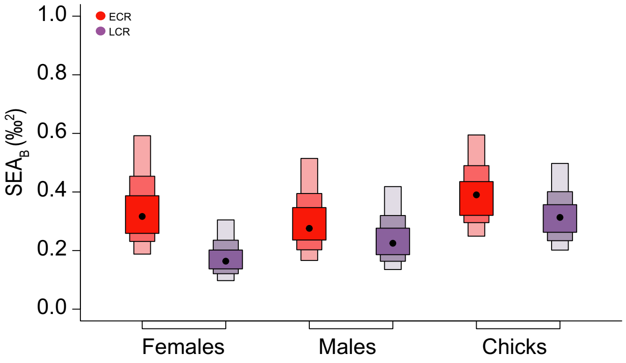

Fig. 3 Bayesian standard ellipse areas (SEA_B, presented in ‰^{2}) for Magellanic penguins' plasma samples from Martillo Island by sex/age (adult females, adult males and chicks) during the chicks rearing period (*ECR* early-chicks rearing in red, *LCR* late-chicks rearing in purple). Black dots correspond to the mode SEA_B for each sex/age group, shaded boxes represent the 50%, 75%, and 95% credible intervals from dark to light color

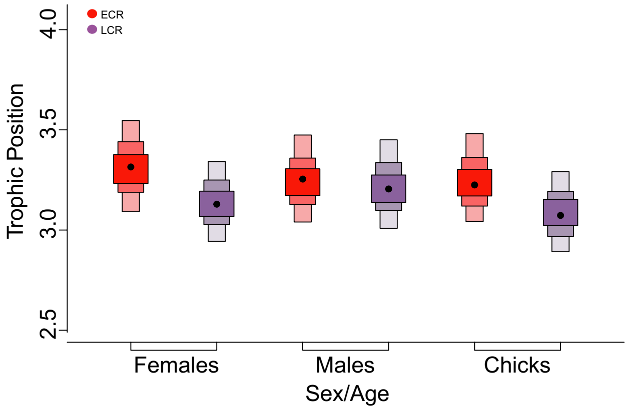

Fig. 4 Trophic Position of adult females, adult males and chicks separated by stage (*ECR* early-chicks rearing in red, *LCR* late-chicks rearing in purple). Black dots correspond to the mode trophic position for each age/colony in each stage; shaded boxes represent the 50%, 75%, and 95% credible intervals from dark to light color

For $\delta^{15}N$ values, we found no support for seasonal consistency in females and chicks ($\delta^{15}N_{females}$: $F_{1,24} = 13.45$, $p < 0.01$; $\delta^{15}N_{chicks}$: $F_{1,41} = 9.52$, $p < 0.01$) while for males we found consistency between the early and late chick-rearing stages ($\delta^{15}N_{males}$: $F_{1,24} = 0.31$, $p = 0.58$). For $\delta^{13}C$ values, we found no support for seasonal consistency between the early and late chick-rearing stages for any sex/age group ($\delta^{13}C_{females}$: $F_{1,24} = 62.07$, $p < 0.01$; $\delta^{13}C_{males}$: $F_{1,24} = 52.96$, $p < 0.01$; $\delta^{13}C_{chicks}$: $F_{1,41} = 123.87$, $p < 0.01$).

Trophic position estimates (population level)

Estimates of TP differed between breeding stages (Fig. 4). For all sex/age group comparisons, we found generally higher TP distribution during early chick rearing relative to the late chick-rearing stage (in 87%, 57%, and 86% of models runs within females, males, and chicks, respectively). Within the ECR stage, adult females generally had higher TP distribution than adult males or chicks (in 68% and 67% of model runs; respectively), and adult males only had higher TP estimates relative to chicks in 50% of model runs. Within the LCR stage, males had higher TP relative to females and chicks in 71% and 81% of model runs; respectively, and females had higher TP relative to chicks in 66% of model runs.

Mixing model analyses (population level)

During the ECR stage, mixing model analyses indicated that prey group 2 (i.e. mid-trophic level, pelagic, and

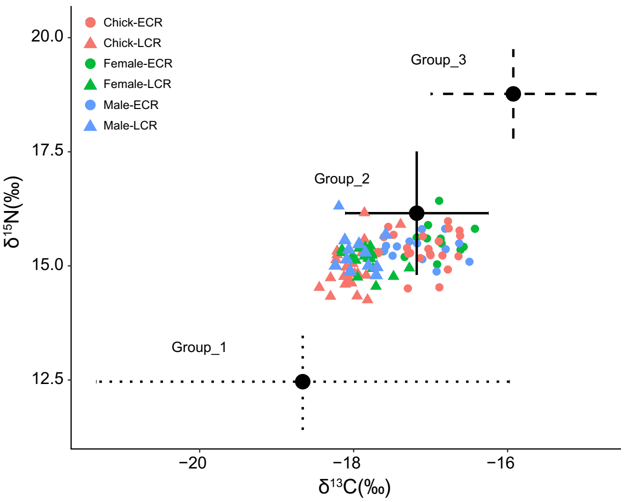

Fig. 5 Isospace plot based on individual δ^{13}C and δ^{15}N values of chicks, adult females and adult males of Magellanic penguins at Martillo Island during chicks-rearing (early and late stages) in 2016 and of their prey sources (average ± SD): group 1 (*Grimothea gregaria*—pelagic), group 2 (*G. gregaria*—benthic, *Sprattus fuegensis*, *Patagonototen tessellata*, *P. ramsayi*) and group 3 (*Eleginops maclovinus, Odontesthes smitti*, *P. cornucola*). Prey stable isotope values are corrected by the trophic discrimination factors estimated by Magellanic plasma samples (Jenkins et al. 2019). References: *ECR* early-chicks rearing, *LCR* late-chicks rearing

bentho-pelagic prey species) represented 100% of the diet of all three sex/age groups (Fig. 5, Table 2). During the LCR stage groups continue to consume prey group 2 (20–50% of diets on average) while increasing the consumption of group 1 (i.e., low-trophic level prey species; 30–50% of diets on average; Fig. 5, Table 2). For both breeding stages, the predicted dietary proportion of prey group 3 (i.e., mid-trophic level coastal prey species) was relatively low (0–30% of diets on average) in all three sex/age groups (Fig. 5, Table 2).

Individual consistency

We found no support for individual consistency, and no support for seasonal consistency for the three sex/ages, with no significant correlations in individual penguin δ^{15}N (Females: $t_{11} = -0.02$ $r = -0.01$, $p = 0.98$; Males: $t_{11} = -0.12$, $r = -0.04$, $p = 0.91$; Chicks: $t_{19} = 1.74$, $r = 0.24$, $p = 0.30$) and δ^{13}C values (Females: $t_{11} = 1.76$, $r = 0.47$, $p = 0.1$; Males: $t_{11} = 0.68$, $r = 0.20$, $p = 0.50$; Chicks: $t_{19} = 1.07$, $r = 0.24$, $p = 0.30$) between stages (Fig. 6).

Family groups

GLMMs indicated a high percentage of variability explained by the random family ID parameter, which represents a high intra-family variability (Table 1). We found higher δ^{13}C and

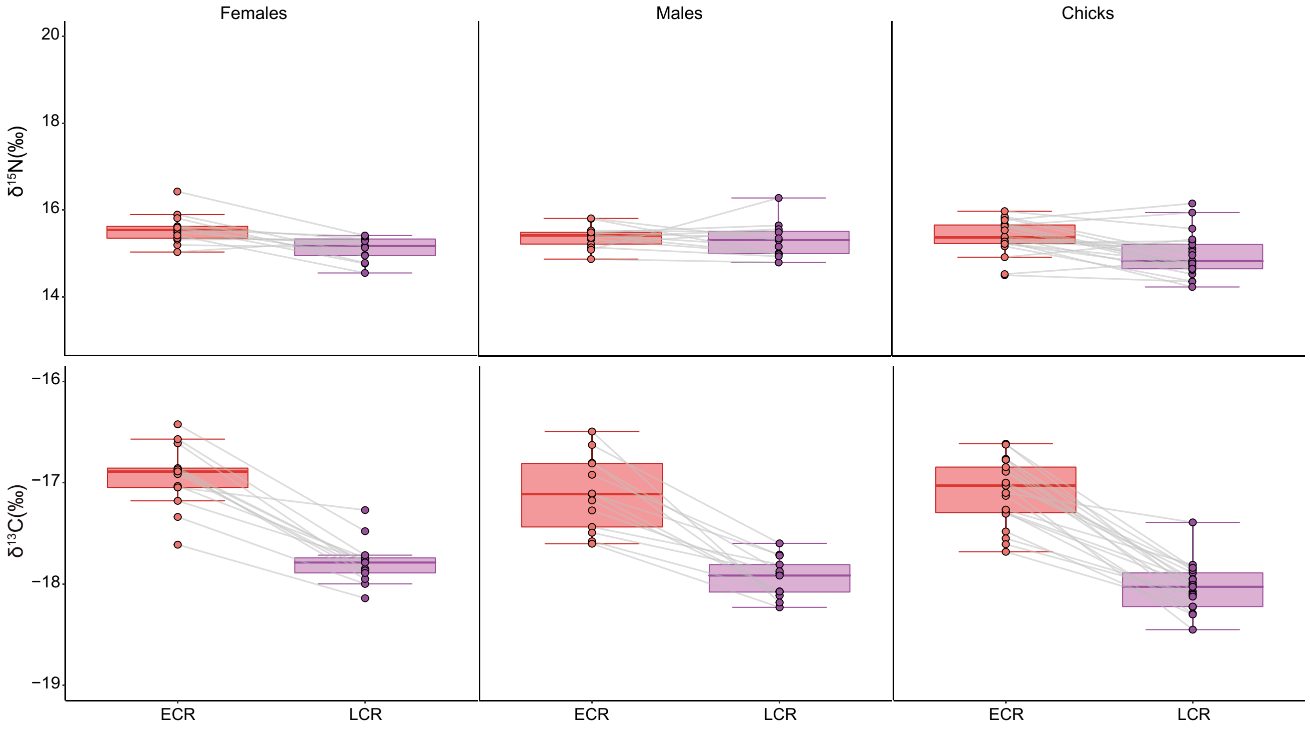

Fig. 6 δ^{15}N and δ^{13}C values for females, males, and chicks of Magellanic penguins from Martillo Island separated by sex/age and chicks rearing period (*ECR* early-chicks rearing, *LCR* late-chicks rearing). Lines connect ECR (red) values and LCR (violet) for each sampled individual

Table 2 Results of MixSIAR Bayesian isotope mixing model showing the mean (95% credibility intervals) diet proportion of prey consumed by adult females (F), adult males (M) and chicks (C) of Magellanic penguins' family groups from Martillo Island during chicks rearing period (early and late stages)

Functional trophic groups	F (early)	F (late)	M (early)	M (late)	C (early)	C (late)
Group 1: *Grimothea gregaria*-pelagic	0.0 (0.0–0.0)	0.3 (0.2–0.5)	0.0 (0.0–0.1)	0.5 (0.2–0.6)	0.0 (0.0–0.1)	0.5 (0.2–0.6)
Group 2: *G. gregaria*- benthic + *Sprattus fuegensis* + *Patagonototen tessellata* + *P. ramsayi*	1.0 (0.9–1.0)	0.5 (0.0–0.8)	1.0 (0.8–1.0)	0.2 (0.0–0.7)	1.0 (0.9–1.0)	0.3 (0.0–0.4)
Group 3: *Eleginops maclovinus* + *Odontesthes smitti* + *Patagonototen cornucola*	0.0 (0.0–0.1)	0.2 (0.0–0.4)	0.0 (0.0–0.0)	0.3 (0.0–0.5)	0.0 (0.0–0.0)	0.2 (0.0–0.3)

δ^{15}N values during ECR relative to LCR in all three sex/age groups (Table 1). The linear relationship between chicks and their parents showed significant differences between them for δ^{13}C values during the ECR stage but the adjusted R^2 value was relatively weak (Table 3). For δ^{15}N, we did not find a linear relationship for any stage between the chicks and their parents indicating that there was no intra-familiar consistency (Table 3).

Finally, Euclidean distance (ED), which is a proxy of diet similarity between chicks and parent, ranged from 0.07 to 2.48 ‰ (mean ± SD: 1.38 ± 0.62) and from 0.04 to 2.35 ‰ (mean ± SD: 1.25 ± 0.59) for chick-female and chick-male pairs during the ECR stage, respectively. While during the LCR stage, ED ranged from 0.17 to 1.90 ‰ (mean ± SD: 1.00 ± 0.44) and from 0.37 to 2.23 ‰ (mean ± SD: 0.98 ± 0.44) for chick-female and chick-male pairs, respectively. For both chick-rearing stages, we found no effect of adult sex on ED (GLMM$_{\mathrm{ECR}}$, estimate = 1.07, SE = 0.17, $t = 5.38$, $p = 0.52$, CI: [0.87–1.31]; GLMM$_{\mathrm{LCR}}$, estimate = 1.04, SE = 0.13, $t = 8.48$, $p = 0.77$, CI: [0.81–1.32]).

Discussion

Our study provides insights into temporal variation in the trophic niche, seasonal and individual consistency, and parental provisioning behaviors in Magellanic penguins during chick-rearing at a breeding colony in the southernmost range of their distribution. Optimal foraging theory suggests that adults should adapt their strategies to maximize foraging efficiency, and therefore, fitness (Pyke et al. 1977). Although the flexibility of foraging is described as a mechanism that increases its efficiency in a variable environment (e.g. Grémillet et al. 2012), there is evidence that individual specialization and behavioral consistency may also be adaptive (Wakefield et al. 2015; Patrick and Weimerskirch 2017). While we found that the isotopic niches of Magellanic penguins differed seasonally between the ECR and LCR stages, there was little to no evidence of individual or sex-specific selective provisioning but high variability within family groups (accounting for 90% of the total isotopic variability).

The results obtained partially refute our hypotheses. Specially, we found support for our predictions of seasonal differences in adults' trophic niche between chick-rearing stages and a lack of seasonal individual trophic consistency. However, we did not find evidence of selective provisioning as was previously reported for this species at colonies in North Patagonia (Ciancio et al. 2018). Magellanic penguins share parental care duties during the brooding period (Boersma et al. 2013) and are opportunistic foragers depending on the season and prey species abundance and availability in the region (Scolaro et al. 1999; Clausen and Pütz 2002). Indeed, at this southern colony, Scioscia et al. (2014) using stomach content reported an inconsistent or irregular difference in diet between sexes within each year and breeding stage, which could explain the high isotopic variability we found within family groups. However, this comparison should be taken with caution due to the mismatch of methodology between Scioscia et al. (2014) and our study (stomach content only provides a snapshot of diet during one foraging

Table 3 Linear model for each stage (ECR: early-chicks rearing; LCR: late-chicks rearing) using chick's stable isotope values (δ^{13}C and δ^{15}N) as response variable and parents' (adult female or adult male) stable isotope values as an explanatory variable. Model structure, Fisher statistic, p-value and R^2 fit are reported for each model

Stage	Model structures	*F*	*p*-value	*R*^{2}
ECR				
	$\delta^{15}\mathrm{N}_{\mathrm{Chick}} \sim \delta^{15}\mathrm{N}_{\mathrm{Female}}$	4.54	0.05	0.14
	$\delta^{15}\mathrm{N}_{\mathrm{Chick}} \sim \delta^{15}\mathrm{N}_{\mathrm{Male}}$	0.31	0.60	-0.03
	$\delta^{13}\mathrm{C}_{\mathrm{Chick}} \sim \delta^{13}\mathrm{C}_{\mathrm{Female}}$	7.59	0.02	0.25
	$\delta^{13}\mathrm{C}_{\mathrm{Chick}} \sim \delta^{13}\mathrm{C}_{\mathrm{Male}}$	9.44	0.00	0.30
LCR				
	$\delta^{15}\mathrm{N}_{\mathrm{Chick}} \sim \delta^{15}\mathrm{N}_{\mathrm{Female}}$	0.00	0.97	-0.05
	$\delta^{15}\mathrm{N}_{\mathrm{Chick}} \sim \delta^{15}\mathrm{N}_{\mathrm{Male}}$	3.00	0.10	0.09
	$\delta^{13}\mathrm{C}_{\mathrm{Chick}} \sim \delta^{13}\mathrm{C}_{\mathrm{Female}}$	0.39	0.54	-0.03
	$\delta^{13}\mathrm{C}_{\mathrm{Chick}} \sim \delta^{13}\mathrm{C}_{\mathrm{Male}}$	0.33	0.57	-0.03

trip while stable isotope values of plasma integrate diet over 15 days period).

Seasonal shifts in foraging habitat were previously reported using SIA in other penguins' species between prebreeding and breeding season, or between breeding and postbreeding season (e.g., little penguins, Kowalczyk et al. 2014; gentoo and Adelie penguins, Herman et al. 2017). However, studies exploring isotopic variation within the breeding season are less common (Gorman et al. 2021). In our study, shifts in foraging habitat use between the ECR and LCR stages, in addition to changes in diet composition, may have influenced the isotopic niches of Magellanic penguins.

Baseline δ^{13}C and δ^{15}N values (e.g., phytoplankton and zooplankton) can change between inshore/benthic and offshore/pelagic habitats and isotopic differences between consumers have also been linked to foraging habitats in space and time (France 1995; Cherel and Hobson 2007; Graham et al. 2010). The inconsistency found in the δ^{13}C and δ^{15}N values of females and chicks between ECR and LCR, and only in δ^{13}C for males could be related to a change in the foraging area used by adults (inshore *vs*. offshore areas), a change in diet composition, or a change in both foraging area and diet composition. Considering that during the LCR stage chicks are larger and require food with less frequency, adults could undertake longer and further away foraging trips (Boersma et al. 2013). Previous GPS studies in this colony have found that adults during this time can use eastward feeding areas outside the Beagle Channel (Raya Rey unpubl. data), also foraging trip duration is used as a proxy of foraging distance which proved to be longer for the LCR (Scioscia et al. 2010), with this region characterized by lower δ^{13}C and δ^{15}N values typically from open waters (Riccialdelli et al. 2020). A change in δ^{13}C and δ^{15}N values between stages may support this explanation for chick and females.

Moreover, our mixing model results suggest variation in diet composition. Adults fed on a mixture of low- and mid-trophic level species during the LCR stage and predominantly on mid-trophic level species during ECR. Specifically, during LCR, we found a shift in both females' and chicks' isotopic niches towards lower isotopic values, lower TP, and a predicted shift in the diet composition increasing the consumption of the pelagic form of *G. gregaria*. This prey species has lower δ^{13}C and δ^{15}N values and occupy lower TPs in comparison to mid-trophic species (group 2, such as the benthic form of *G. gregaria*, *S. fuegensis*, *Patagonotothen spp*) (TP ~ 2.0 vs TP ~ 3.0, respectively, Riccialdelli et al. 2020), consequently, this change in the prey choice also explained the trophic shift observed during the LCR. For males, the consistency in δ^{15}N values and TPs between stages complicates the interpretation. Although the shift in δ^{13}C values may reflect a change in foraging areas, as supported by previous GPS data, we can also assume a consistency in the type of prey chosen by them during each stage, mobile and high trophic level prey. However, when we explore the diet composition, we found the same differences reported for females and chicks. We acknowledge that we may have some important prey missed in our study, such as squids (e.g., *Doryteuthis gahi*), which are common prey for Magellanic penguin (Scioscia et al. 2014). This squid species exhibits inshore-offshore migrations and can enter into the channel through the east mouth for reproduction (Rosenfeld et al. 2014) and larval development (Presta et al. 2023). Their contribution to the diet of adults may have implications for mixing model results.

However, with our data is it not possible to conclusively determine if a change in the foraging area, change in the diet composition, or a combination of these two factors are the most significant drivers of isotopic variation. To address this limitation, future studies should combine SIA with GPS tracking at each stage and sample a more comprehensive list of prey taxa.

The plasma stable isotope-based mixing model results for the ECR differ from those reported in a previous analysis using whole blood stable isotope values during the chick-rearing period at the same colony. Using a whole blood stable isotope-based mixing model, Dodino et al. (2022) suggest that adults and chicks from Martillo Island fed mainly on *G. gregaria*-pelagic (prey group 1) during the ECR period, similar to what our plasma stable isotope-based mixing model results suggest for the LCR period. This is likely related to the fact that the whole blood integrates diets over a ~ 30 days period (Hobson and Clark 1992; Barquete et al. 2013), and consequently when collected during the ECR stage could also integrate dietary information from the late incubation stage. However, despite these differences between studies using plasma vs. whole blood stable isotope values, both studies indicate that adults feed their offspring the same diets compositions that they consume for themselves. In addition, we found broadly similar isotopic niches among sexes in both stages suggesting that sexual dimorphism and different diving capacities of Magellanic penguins from Martillo Island do not influence diets and food provisioning during chick-rearing as previously found for the diving behavior in the same colony (Raya Rey et al. 2012a).

Prey availability could influence adults' prey choice and provisioning behaviors (Waluda et al. 2012; Horswill et al. 2017; Dodino et al. 2020). In addition, the size and the energy density of prey item can be a factor, since larger prey items could be more difficult for a chick to digest than a smaller one and also chick growth rates is influenced by the caloric content of prey (Van Heezik and Davis 1990). Diez et al. (2018) reported that *G. gregaria* is present all year round with similar abundance in the Beagle Channel. In addition, *G. gregaria* is the smallest and the highest energy density prey (50–70 mm, 11.0 kJ g^{-1}, respectively, Ciancio et al. 2007) in comparison with many of the prey species within group 2 (e.g., *S. fuegensis*: 35–140 mm, 7.15 kJ g^{-1}; *P. tesellata*: 118–120 mm, 4.0 kJ g^{-1}; *P. ramsayi*: 60–140 mm, 4.8 kJ g^{-1}; size and energy density respectively, Ciancio et al. 2007). In this sense, it is interesting to notice with this study that adults only selected prey group 2 during the LCR. One explanation of these new founds could be related to a potential lower digestibility of this prey, which could affect breeding success during an early chick-rearing stage. In this sense, it is suggested that chicks grow at a reduced rate with a diet based on this prey item (Thompson 1993). However, the change in the diet composition during the LCR stage may not have as large of an impact on chick survival since the chicks are bigger and their energy requirements are lower relative to the ECR stage.

Individual niche variation is frequently found within generalist populations and is commonly assessed by quantifying the degree of inter-individual foraging variation and the presence of individual consistency over time (Bolnick et al. 2003; Sargeant et al. 2007). Magellanic penguins are a generalist population and at Tierra del Fuego showed different foraging behavior between neighboring colonies (related to chicks' requirements and the spatial distribution of prey, Dodino et al. 2022) and between years (related to changes in prey availability, Dodino et al. 2020). In this sense, it was expected that Magellanic penguins' population at Martillo Island would have little to no individual consistency in their trophic niche and a high variability within family groups. Future research on individual foraging specialization in this species across their breeding distribution is needed to identify the potential environmental mechanisms that may act to mediate the degree of individual variation within these generalist populations.

Finally, for a better understanding of trophic consistency Magellanic, future studies could extend the present work over years to evaluate inter-annual consistency in the feeding sites chosen during each chick-rearing stage. While not possible to assess using our current dataset, if resources are spatiotemporally correlated a 'win-stay, lose-shift' tactic could be optimal such that potential fidelity to feeding areas in each stage could be associated with prior success (Switzer 1993; Schmidt 2001; Piper 2011; Spencer 2012).

Implications

Site-based conservation is a key strategy for protecting biodiversity worldwide (Watson et al. 2014). Identifying the spatial use of Magellanic penguins at the Beagle Channel during the chick-rearing period highlights the critical habitats used by this species, which is crucial for planning marine protected areas networks.

Identifying the prey items that Magellanic penguins chose for themselves and their chicks is important in the context of global climate change. Since changes in environmental conditions (i.e., variability in sea surface temperature, chlorophyll a, etc.) could affect the availability and/or the contamination exposure of important penguin prey item. For example, harmful algal blooms that can cause massive fish to die off, contaminate seafood with toxins, or detrimentally alter ecosystem function have been increasing in frequency, magnitude, and duration worldwide (Glibert et al. 2014) and the Beagle Channel is not an exception (Almandoz et al. 2019). The effects of climate change on Magellanic penguins' prey can have important consequences on penguins foraging and breeding success, and ultimately population growth. Knowledge of the plasticity of Magellanic penguins foraging habitats during the chick-rearing period is crucial to understand how they could respond to these increasingly frequent events.

Finally, the application of the ED method, proposed by Ciancio et al. (2018), to quantify the sex-related differences in parental provisioning provide a quick and easy way to quantify sex-related differences in species that share parental duties as Magellanic penguins. Information about their plasticity food provisioning along their breeding distribution is little known and could have conservation implications. For example, it can allow us to assess their adaptive capacity in the face of changes in the availability of their prey due to natural global changes or anthropogenic effects, such as fishing.

Conclusion

This study improves our understanding of chick provisioning behaviors and age, sex, and breeding stage-specific trophic niches of Magellanic penguins. Despite Magellanic penguins being considered as less concern in the red list of the IUCN, as long-lived species living in an unpredictable environment, knowledge of species diets and foraging plasticity is central for projecting how they may respond to future environmental change (i.e., changes in prey availability, change in the contamination exposure of their key prey items, etc.). Finally, knowledge of the potential prey and areas that adult penguins choose to feed themselves and their offspring could have key implications for the marine spatial planning at the Beagle Channel ecosystem, which currently does not have regulation.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s00227-023-04242-z.

Acknowledgements We would like to thank Maria Eugenia Lopez, Analía San Martin and Hernan Sacristan for their help during the fieldwork. Also, we thank Hayat Bennadji, Ulises Balza, and Nicolás A. Lois for technical help with stable isotope analysis. We acknowledge Andres and Alejandro Greco from Piratur SA for transportation to Martillo Island; and the Centro Austral de Investigaciones Científicas (CADIC), Museo Acatushún de Aves y Mamíferos Marinos Australes, and Ea. Harberton, which provided logistical support.

Author contributions SD: conceptualization, methodology, formal analysis and investigation, writing-original draft preparation; LR: conceptualization, methodology, investigation, resources, writing-review and editing, supervision; MJP: methodology, resources, writing-review and editing; KP: resources, writing-review and editing, funding acquisition; ARR: conceptualization, methodology, investigation, resources, writing-review and editing, supervision, project administration, funding acquisition.

Funding This study was financially supported by the Agencia Nacional de Promoción Científica y Tecnológica (PICT 2012-1832, PICT 2014-1870), Wildlife Conservation Society, Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), and the Antarctic Research Trust. Research by S.D. was carried out under a Ph.D. fellowship from CONICET.

Data availability Penguins' stable isotope raw data could find available here: https://ri.conicet.gov.ar/handle/11336/197811

Declarations

Conflict of interest The authors have no relevant financial or non-financial interests to disclose.

Ethical approval All applicable international, national, and/or institutional guidelines for the care and use of animals were followed.

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