



# Within- and among-colony variation in non-breeding dispersion of Magellanic penguins breeding along the coast of Argentina

Melina Barrionuevo<sup>1,\*</sup>, Esteban Frere<sup>2,3</sup>, Flavio Quintana<sup>4</sup>, Javier Ciancio<sup>5</sup>, Nahuel Marchisio<sup>2</sup>, Simeon Lisovski<sup>6</sup>

<sup>1</sup>Instituto de Investigaciones en Biodiversidad y Medioambiente, Universidad Nacional del Comahue, 8400 Bariloche, Argentina

<sup>2</sup>Centro de Investigaciones Puerto Deseado, Universidad Nacional de la Patagonia Austral, CONICET, 9050 Puerto Deseado, Argentina

<sup>3</sup>Wildlife Conservation Society, C1426AKC CABA, Argentina

<sup>4</sup>Instituto de Biología de Organismos Marinos, CONICET, 9120 Puerto Madryn, Argentina

<sup>5</sup>Centro para el Estudio de Sistemas Marinos, CONICET, 9120 Puerto Madryn, Argentina

<sup>6</sup>Alfred Wegener Institute Helmholtz, Centre for Polar and Marine Research, Polar Terrestrial Environmental Systems, 14473 Potsdam, Germany

**ABSTRACT:** Magellanic penguins *Spheniscus magellanicus* are upper trophic level predators and play a key role within their marine ecosystems. However, we lack detailed understanding of their non-breeding distribution where they might be impacted by human threats and climate change. Using geolocator tracking devices deployed in 2021, we analyzed individual non-breeding movements, and differences in the spatial, environmental, and trophic niches of Magellanic penguins breeding along the Atlantic coast of Argentina. The results show that movement characteristics, including trip lengths and dispersal distance, were similar among individuals and across colonies. However, the temporal pattern, including the timing of arrival to the breeding sites, differed between colonies. During the non-breeding season, distributions showed considerable overlap between colonies, notably between individuals from the central and the northernmost breeding sites. Individuals from the northern and central colonies faced similar oceanographic features (i.e. sea surface temperature, chlorophyll *a*, salinity, depth) and used similar foraging niches while within the anchovy geographic domain. In contrast, individuals breeding farther south were feeding within the geographically distinct sprat domain. Our results indicate that Magellanic penguins breeding along the latitudinal range of Argentina express a broad variation in habitat use during the non-breeding period, and make use of a large proportion of the Patagonian Shelf. The latitudinal location of the breeding colony seems to define the trophic niche and where individuals move during the non-breeding season.

**KEY WORDS:** *Spheniscus magellanicus* · Migration · Habitat use · Geolocation · Stable isotopes

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## 1. INTRODUCTION

In marine ecosystems, dispersion during the non-breeding period is a widely adopted strategy to follow resources which, in turn, respond to large-scale

currents and ocean surface temperatures (Campana et al. 2006, Louge et al. 2009, Fagan 2019). However, on a small scale, spatial or trophic segregation within and among species may also be modulated to avoid competition (Phillips et al. 2004,

\*Corresponding author:  
melinabarrionuevo@comahue-conicet.gob.ar

González-Solís et al. 2007). For example, different *Eudyptes* penguin species breeding in close proximity stay in the same areas during the non-breeding season but exploit different trophic niches (Thiebot et al. 2012, 2013, Ratcliffe et al. 2014a), while individuals of the same species form clusters according to their breeding colonies and consume similar resources but avoid spatial overlap (Thiebot et al. 2011, 2012, Ratcliffe et al. 2014a). Thus, in *Eudyptes* penguins, the location of the breeding colony seems to be a major factor defining migration routes (Thiebot et al. 2013). This is likely driven by population-specific foraging strategies and different breeding phenologies, resulting from adaptations to local conditions (Rayner et al. 2011).

The population of Magellanic penguins *Spheniscus magellanicus* consists of approximately 2 million mature individuals (BirdLife International 2020). In Argentina, ~66 colonies are distributed uniformly along a 1200 km latitudinal range, from 41 to 54° S (García-Borboroglu et al. 2022, Millones et al. 2022). This area is characterized by the Patagonian Continental Shelf (waters south of 40° S), which is part of the larger South American Shelf that includes areas off southern Brazil, Uruguay, and Argentina (Gil et al. 2019). The Patagonian Continental Shelf is known to be one of the world's most productive marine areas and is a well-known important area for different seabird species during the non-breeding season (Falabella et al. 2009, Copello et al. 2013, Blanco et al. 2017). During this period, Magellanic penguins use the shelf areas and move up to 1000 km northwards (Pütz et al. 2007, Yamamoto et al. 2019, Barrionuevo et al. 2020, Dodino et al. 2021). Previous tracking studies showed that during the non-breeding season, individuals from the same colony segregate by sex, with females dispersing farther north compared to males (Yamamoto et al. 2019). However, males tend to move farther offshore (Barrionuevo et al. 2020). In addition, males seem to forage in a different trophic niche compared to females (Barrionuevo et al. 2020, Dodino et al. 2021).

Here we aimed to quantify the extent of spatial, environmental, and trophic niche segregation within and among colonies of Magellanic penguins during the non-breeding season. In 2021, we collected data from individuals belonging to 3 colonies distributed across their latitudinal breeding range in the southwest Atlantic. Furthermore, based on individual movements, we aimed to identify important areas of use for the species within the South American Shelf. We predicted that penguins from the different colonies would exhibit similar movement patterns, leading to

spatial–temporal segregation along a latitudinal gradient, and that individuals from different colonies would experience different environmental conditions and resources during the non-breeding season.

## 2. MATERIALS AND METHODS

### 2.1. Study species and sites

Adult Magellanic penguins arrive at their breeding colonies from late September to early October. Adult breeders attempt to breed only once per breeding season, and usually show site fidelity, nesting in the same area as in previous years. Nestlings fledge around February. After breeding, Magellanic penguins conduct a pre-molting trip and molt all feathers during March and then start their migration. Their known non-breeding distribution within the Atlantic Ocean ranges from southern Patagonia to Uruguay and Brazil (Yamamoto et al. 2019).

Our study was conducted at 3 distinct breeding colonies in Argentina: Estancia San Lorenzo (SL: 42° 05' S, 63° 54' W) (north), Isla Quiroga (IQ: 47° 45' S, 65° 53' W) (central), and Cabo Vírgenes (CV: 52° 21' S, 68° 23' W) (south). The colonies are separated by 636 (SL–IQ), 530 (IQ–CV), and 1166 km (SL–CV). During the breeding period, Argentine anchovy *Engraulis anchoita* constitute the main prey for the northern SL population, CV penguins in the south feed on Fuegian sprat *Sprattus fuegensis*, and the central IQ colony is located between the 2 domains, and these birds eat mostly sprat and Patagonian squid *Loligo gahi* (Ciancio et al. 2021). SL is the largest of the 3 breeding populations, with 204 416 breeding pairs, followed by CV (127 492) and IQ (1348, but 24 234 pairs within a 10 km radius) (García-Borboroglu et al. 2022, Millones et al. 2022). Among the ~66 colonies in Argentina, SL is the largest, CV is the third largest, and IQ with its surrounding sites represents an average-size colony. Since the 1990s, the population of the SL colony has increased by 92%, and the CV colony experienced a population increase by about 42%, while the IQ population has remained relatively stable (García-Borboroglu et al. 2022, Millones et al. 2022).

### 2.2. Movement analysis

Between January and March 2021, we deployed 37 geolocators (MK3 and MK4, 1.8 and 2.5 g, Lotek, UK) on Magellanic penguins (IQ: 14, SL: 14, CV: 9 geo-

locators). During October 2021, penguin colonies were revisited and geolocators were retrieved. Loggers were deployed on adults with previous known breeding attempts. In January and February, penguins were feeding nestlings, and in March they were molting; we only analyzed the data from April to September, excluding the pre-molting trip. Sex was identified by bill length and depth, measured with a caliper ( $\pm 0.1$  mm, Mitutoyo) (Gandini et al. 1992). Geolocators were attached to the legs with cable ties as recommended by Ratcliffe et al. (2014b). The tags record light intensities every minute and store the maximum light level per 5 min period. In addition, the loggers stored saltwater immersion data (MK4: a value of 0 indicates that the logger was dry for 10 m during each 1 s interval measurement, while 1 indicates that it was completely immersed. MK3: binary switch between wet/dry if the condition lasts longer than 6 s). Departure and arrival dates were obtained from the wet/dry records. Departure was defined as the day when the recordings were continually wet for more than 6 h, with dry events no longer than 30 min, and arrival when recordings were continuously dry for 6 h. MK3 also recorded temperature after 25 min of continuous wet conditions.

Light recordings were downloaded using the BioTrack software and decoded using the Bastrack software 'decompressor' (BioTrack 2013). Using the package 'TwGeos' (Lisovski et al. 2015) in R (R Development Core Team 2021), we defined twilight events (sunrise/sunset) via the threshold method (choosing a threshold of 1.5 arbitrary light units). For each individual, calibration periods were identified to estimate the zenith angle and the twilight error distribution that corresponds to the chosen light threshold based on the light recordings during periods after logger deployment and before logger retrieval (for more details, see Lisovski et al. 2020). We developed a 3-step process to refine location estimates and derive the most likely tracks and spatial credibility intervals. (1) Since the calibrated zenith angle provides a rough estimate only, which is likely not representative for the non-breeding season (e.g. short calibration periods with many sunrise/sunset times in breeding burrows), we estimated individual zenith angle corrections; initial threshold paths with a correction factor for the calibrated zenith angle ( $-1^\circ$  to  $1^\circ$  by  $0.2^\circ$ ) were calculated, and the correction angles that resulted in the lowest variance in latitudes during the equinox periods were chosen (Lisovski et al. 2020). (2) Next, to remove initial estimates on land, we calculated 1000 possible migration paths using the threshold methods and changing the

twilight times using the calibrated twilight error distribution, resulting in 1000 location estimates per twilight event that represent the expected spatial distribution of possible locations. In a forward loop, we then moved location estimates of the initial track (estimated using the annotated twilight times and the zenith angle correction) that are on land to the closest possible location at sea from the 1000 possible location estimates. (3) Finally, we used the R package 'SGAT' and the implemented Bayesian Markov chain Monte Carlo (MCMC) methods to refine movement paths including prior information on the expected twilight error distribution (calibration), a spatial mask, and a movement model. The spatial mask not only included ocean/land restriction but also a probability of locations based on the sea surface temperature (SST) measured by the tag and the daily modeled SST from the NOAA OI SST V2 High Resolution Dataset provided by the NOAA Physical Sciences Laboratory (Boulder, CO; <https://psl.noaa.gov>). The movement model was defined by a gamma distribution with scale and rate parameters (0.2, 0.25). The model was tuned using a relaxed twilight model ('ModifiedGamma' model) and 1000 iterations before running a final 'Gamma' model with 2000 iterations. Most likely tracks (median) and confidence intervals (95% CI) were calculated by summarizing the resulting 2000 MCMC chains. In addition, we compiled maps of relative time spent for each colony including all 2000 MCMC chains of individuals. Relative time spent maps indicate the spatial distribution of the tracked individual incorporating the uncertainty of the geolocation method. All final MCMC chains were used, and numbers of locations were counted within each cell of a spatial grid (resolution was set at 0.25) and normalized to the time span of the entire track. The sum of all cells thus corresponds to the time period from start to end of the migration. Overlap in spatial distributions between colonies was calculated taking the density distribution (e.g. the relative time spent calculations) into account (see Broennimann et al. 2012 for details).

To calculate trip metrics, we used established methods from the R package 'track2KBA' (Beal et al. 2021) applied to the most likely track per individual; the 'tripSplit' and 'tripSummary' functions were applied to calculate total distance traveled and maximum distanced reached. To compare trip metrics among colonies, we ran linear models (LMs) with arrival/departure dates (as 'day of the year'), and total distance and maximum distance traveled as response variables and colony as predictor factor.

### 2.3. Oceanographic variables

To investigate potential differences in oceanographic variables experienced by the individuals from the different colonies during the non-breeding season, we extracted the following information for the estimated most likely tracks; SST with a weekly temporal resolution and 1 degree spatial resolution (NOAA OI SST V2 High Resolution Dataset, <https://psl.noaa.gov>), bathymetry (depth) with a 1 arc minute spatial resolution (Amante & Eakins 2009), salinity with a weekly temporal and  $0.25^\circ \times 0.25^\circ$  spatial resolution (Copernicus Marine Service, <https://marine.copernicus.eu/>), and chlorophyll *a* (chl *a*) with  $1080 \times 2160$  global 8 d grids and 1/6 of a degree resolution (Behrenfeld & Falkowski 1997). To quantify differences between colonies, we ran separate linear mixed models (LMMs) using the R Package 'lme4' (Bates 2010), with ID and month as random factors, colony as a predictor variable, and SST, log-transformed chl *a*, salinity, and ocean depth (binomial:  $0 < 200$  m,  $1 \geq 200$  m) as response variables.

To identify the environmental space of individuals experienced during slower movements and thus in areas that might be favorable for e.g. food availability, we calculated the first-passage time (FPT) (i.e. the amount of time spent at each location across the trip; Fauchald & Tveraa 2003). FPT was calculated using the R package 'adehabitatLT' (Calenge 2019) and the function 'FPT' with a transition radius of 150 km, due to the error of the geolocators. We applied LMMs with month and ID as random factors, to quantify the effects of the different above-described oceanographic variables on the individual- and colony-specific log-transformed FPT. Colony was the predictor factor, and multicollinearity between variables was assessed via the variance inflation factor (VIF).

### 2.4. Trophic niche

Blood samples (0.5 ml) were taken from the metatarsal vein of adults returning to the colony in spring. Blood samples were preserved in 70% ethanol prior to  $^{13}\text{C}$  and  $^{15}\text{N}$  stable isotope analysis. Stable isotopes in blood cells and plasma are used as a proxy for the diet over the previous month (Barquete et al. 2013). Prior to the isotope measurement, samples were dried at  $60^\circ\text{C}$  for 48 h and ground. Stable isotope analysis was carried out in the Stable Isotopes Facility at the University of California, Davis, CA. The ratios of stable isotopes were measured

against the reference standards Vienna PeeDee Belemnite for  $^{13}\text{C}$  and atmospheric air for  $^{15}\text{N}$ , which were expressed in  $\delta$  notation in ‰:  $X = [(R_{\text{sample}}/R_{\text{standard}}) - 1]$ , where  $X$  is  $\delta^{13}\text{C}$  or  $\delta^{15}\text{N}$  and  $R$  is the corresponding ratio  $^{13}\text{C}/^{12}\text{C}$  or  $^{15}\text{N}/^{14}\text{N}$ . Mean SD for reference materials (nylon, bovine Liver, USGS-41 glutamic acid, chitin, amaranth flour, caffeine, enriched alanine, keratin, glutamic acid) were 0.07 and 0.08 for  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ , respectively.

We compared the 2-dimensional isotopic niche (Newsome et al. 2007) between the 3 colonies using the R package 'SIBER' (Jackson et al. 2011). To quantify the proportion of Argentine anchovy and Fuegian sprat in the diet of the sampled Magellanic penguins, we used the isotopic Euclidean distance in the respective isotopic space (Ciancio et al. 2021). The smaller the Euclidean distance to a prey, the larger the contribution in the diet of the penguin (see Ciancio et al. 2021 for details). Bayesian isotopic standard ellipse areas (SEAb, contains 39% of data) were fitted to data for each colony. The model was applied with 20 000 iterations and 1000 initial discards. The last 18 000 iterations were thinned by a factor of 10. The overlap between colony isotopic niches was estimated using the function 'maxLikOverlap' in the R package 'SIBER' and presented in percentage overlap. A 1-way ANOVA was used to compare  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  among the 3 colonies.

## 3. RESULTS

Out of the 37 deployed tags, 2 tags from SL and 2 from IQ could not be retrieved. In addition, 2 tags from SL did not record data due to battery failure. Our analysis is thus based on 10 tracks from SL (3 males, 7 females), 12 tracks from IQ (6 males, 6 females), and 9 tracks from CV (4 males, 5 females). The average of all standard deviations of location estimates was 80.72 km for latitude and 79.03 km for longitude.

### 3.1. Non-breeding spatial dispersal

In general, individuals from all 3 colonies traveled north, making use of almost the entire Patagonian Shelf during the non-breeding period (Fig. 1a,b).

Penguins from SL, the northern colony, frequently reached the La Plata River Estuary ( $\sim 36^\circ\text{S}$ ) and Uruguay (6 out of 10 penguins), staying mostly in El Rincón Estuary ( $\sim 40^\circ\text{S}$ ). Only 2 penguins moved farther north to the border between Uruguay and

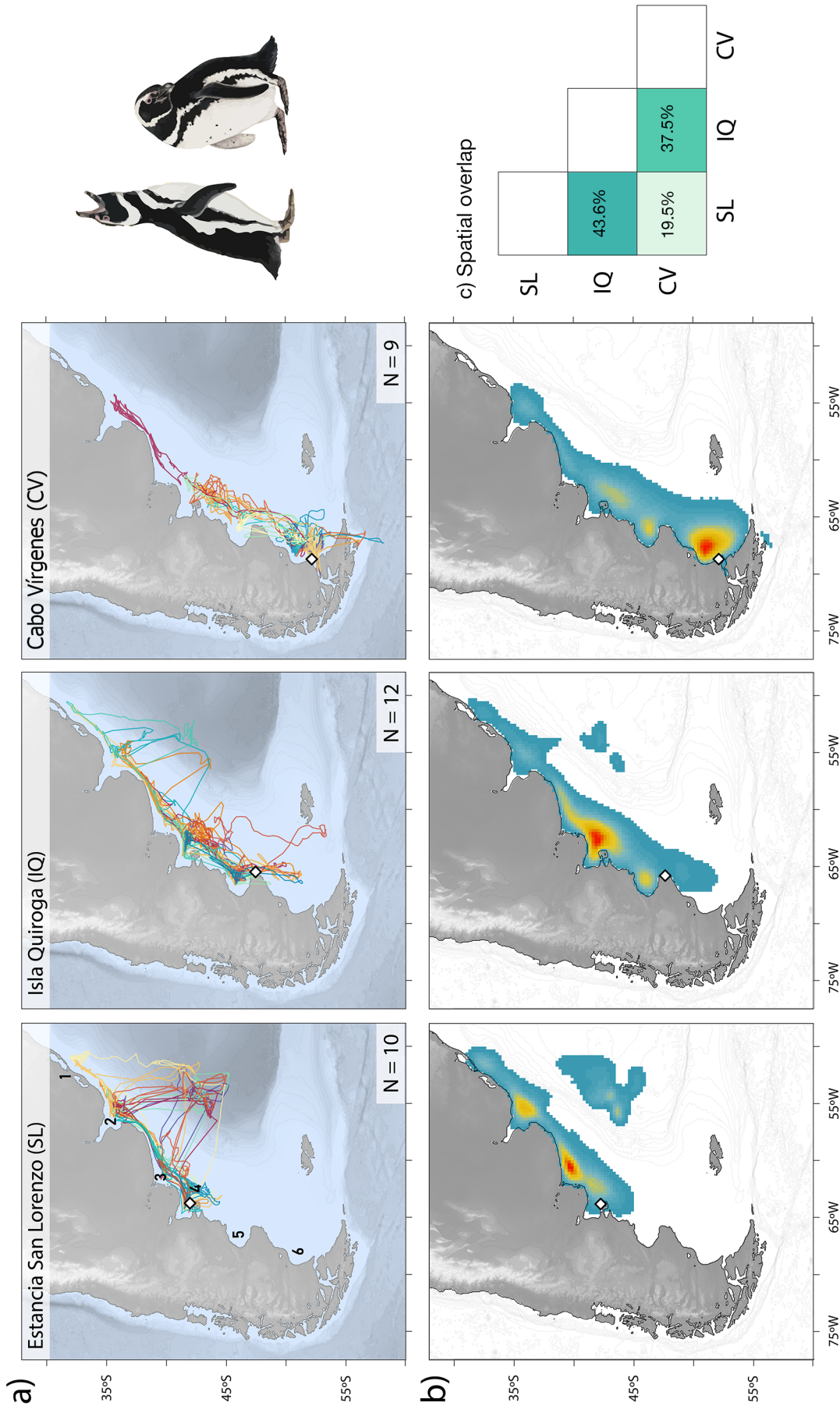


Fig. 1. Non-breeding dispersion of Magellanic penguins from 3 different breeding colonies (white diamonds). Penguins were tracked from March to October using light-level geolocators. (a) Individual tracks (represented by separate colors). The light blue region off the coast of Argentina, Uruguay and southern Brazil highlights the South American Shelf region; waters south of 40° S, which are included in the South American Shelf, form part the Patagonian Shelf. Numbers refer to locations: (1) border between Uruguay and Brazil, (2) La Plata River estuary (~36° S), (3) El Rincón estuary (~40° S), (4) Peninsula Valdés (~42° S), (5) Golfo San Jorge (~46° S), and (6) Bahía Grande (~49–52° S). (b) Relative time spent along the coast, indicating the highest densities (red) of estimated locations and the precision of location estimates. (c) Spatial overlap during the entire breeding season between colonies. SL: San Lorenzo; IQ: Isla Quiroga; CV: Cabo Vírgenes. Magellanic penguin drawing modified and used with permission from the artist Leigh Wolfaardt. Maps made with Natural Earth and ETOPO1 (Amante & Eakins 2009)

Brazil. Two individuals stayed in the surroundings of the colony during the entire non-breeding period (Fig. 1a). Six of the 10 penguins returned to their colonies, using offshore waters outside the Patagonian Shelf in front of Peninsula Valdés (~42° S) between July and September (Fig. 1a,b).

Four of 12 penguins from IQ, the central colony, started with a short trip to the south before moving northwards (Fig. 1a). Two penguins made short trips to the Uruguayan–Brazilian border, while 3 moved as far as La Plata River Estuary waters. Seven individuals stayed in front of Península Valdés during the entire non-breeding period (Fig. 1a).

One of the 9 penguins from CV, the southern colony, traveled north to 40° S (i.e. El Rincón Estuary). Three individuals stayed within Bahía Grande (~49–52° S), and 3 traveled to Peninsula Valdés (~42° S) and Golfo San Jorge (~46° S) (Fig. 1a).

Colonies partially overlapped in the areas used during the non-breeding period. IQ and SL, and IQ and CV shared less than half of the space used (43.6 and 37.5%, respectively). In contrast, the overlap in space between individuals from CV and SL was considerably lower (19.5%, Fig. 1c).

Mean arrival date to the colonies was 25 September (day of the year:  $267.83 \pm 6.60$ ). However, penguins from CV arrived earlier compared to the other colonies: 10.8 d before penguins from IQ (LM:  $t = 4.86$ ,  $p < 0.001$ ) and 6.9 d earlier than SL penguins ( $t = 2.98$ ,  $p = 0.01$ ). On average, individuals from IQ arrived the latest (IQ vs. SL:  $t = -1.86$ ,  $p = 0.07$ )

(Table 1). Departure date was similar among colonies (mean date 9 April, Table 1). Similarly, movement characteristics including the maximum distance traveled from the colony (mean  $\pm$  SD =  $1150 \pm 515$  km), and the total distance traveled (mean  $\pm$  SD =  $6741 \pm 2211$  km) during the non-breeding dispersion, did not differ significantly among colonies (Table 1).

### 3.2. Oceanographic variables

Penguins from the 3 colonies used areas with slight differences in oceanographic features (Table S1, Fig. S1 in the Supplement at [www.int-res.com/articles/suppl/m721p151\\_supp.pdf](http://www.int-res.com/articles/suppl/m721p151_supp.pdf)). SST, chl *a*, and bathymetry differed among colonies (LMM; SST:  $\chi^2 = 54.46$ ,  $p < 0.001$ ; chl *a*:  $\chi^2 = 22.11$ ,  $p < 0.001$ ; bathymetry:  $\chi^2 = 11.93$ ,  $p = 0.003$ ), in contrast to salinity ( $\chi^2 = 1.73$ ,  $p = 0.42$ ) (Table S2). Penguins from CV used shallower waters compared to individuals from the other colonies. Individuals from SL experienced warmer SSTs within more productive waters (high chl *a* concentration) compared to individuals from IQ and CV. Among the latter, tracked penguins from IQ experienced slightly warmer ocean temperatures and stayed within more productive waters (Table S2).

For individuals from CV, the time spent within an area (FPT) increased at low SST and chl *a*, as well as with lower salinity. For individuals from SL and IQ, FPT increased with deeper waters, high SST, and lower chl *a* and salinity (Fig. S2, Table S3). FPT varied with the interactions between oceanographic parameters and colony location (LMM; salinity:  $\chi^2 = 31.94$ ,  $p < 0.001$ ; chl *a*:  $\chi^2 = 643.32$ ,  $p < 0.001$ ; depth:  $\chi^2 = 328.11$ ,  $p < 0.001$ ; SST:  $\chi^2 = 827.63$ ,  $p < 0.001$ ; Fig. S2, Table S3). SSTs experienced by SL and IQ penguins were within the temperature ranges favoring anchovy, while the SST experienced by CV penguins was in the temperature range of sprat (Fig. 2).

### 3.3. Trophic niche

Colony had a significant effect on  $\delta^{13}\text{C}$  (ANOVA:  $F_{2,29} = 28.22$ ,  $p < 0.001$ ) and  $\delta^{15}\text{N}$  ( $F_{2,29} = 8.32$ ,  $p = 0.001$ ) stable isotope values measured in blood of Magellanic penguins (Table 2). The

Table 1. Estimates of the model of the non-breeding dispersion trip metrics (response variable) of the 3 studied colonies (predictor variable) of Magellanic penguins. The intercept is the Cabo Vírgenes (CV) colony, so the difference in the mean parameters between this and the other 2 colonies are shown. The statistics results of linear models are presented. SL: Estancia San Lorenzo; IQ: Isla Quiroga

		CV (Intercept) N = 9	IQ N = 12	SL N = 10	F	df	p
Total distance covered (km)	Mean	6117	302	1493	1.36	3, 27	0.27
	2.5 %	4596	-1658	-718			
	97.5 %	7722	2243	3519			
Maximum distance reached (km)	Mean	1057	256	-17	0.86	3, 27	0.43
	2.5 %	668	-229	-512			
	97.5 %	1441	747	446			
Departure date (Day of the year)	Mean	99.4	-0.3	-1.4	0.04	3, 29	0.96
	2.5 %	92.8	-8.3	-9.2			
	97.5 %	105.2	7.8	7.2			
Arrival date (Day of the year)	Mean	261.6	10.8	6.9	11.9	3, 27	<0.001
	2.5 %	258.2	6.6	2.1			
	97.5 %	264.8	15.8	11.3			

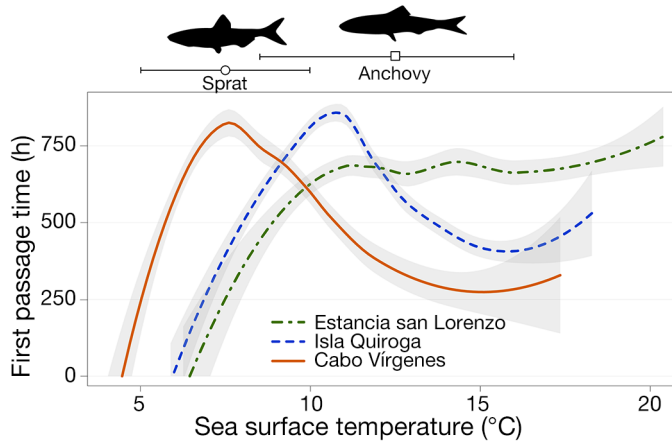


Fig. 2. Smoothed first-passage time (in hours) versus sea surface temperature (SST). Peaks in first-passage time indicate slower movements and can thus be seen as a proxy where tracked penguins found favorable environmental conditions and food. The 2 top bars represent the range and mean thermal preference of the 2 major prey species: sprat (mean: 7.5°C; range: 5–10°C; Madirolas et al. 2000, Allegra et al. 2019) and anchovy (mean: 12.5°C; range: 8.6–16°C; Hansen et al. 2001)

overlap of the isotopic niche (SEAc) mirrored the results of spatial overlap between colonies: higher overlap between individuals breeding in IQ and SL colonies (34%, Table 2, Fig. 3a). However, the isotopic niche (SEAb) did not significantly differ between colonies (Fig. 3b). Penguins breeding at SL and IQ colonies relied more on anchovy (Euclidean distance to anchovy smaller than the distance to sprat) and CV birds relied more on sprat during the last month at sea before the breeding season (Table 2), similar to the spatial overlap analogies.

#### 4. DISCUSSION

During the non-breeding season, Magellanic penguins from different colonies showed similar movement characteristics with regards to the total and maximum distance traveled. However, differences were found in their movement phenology and spatial

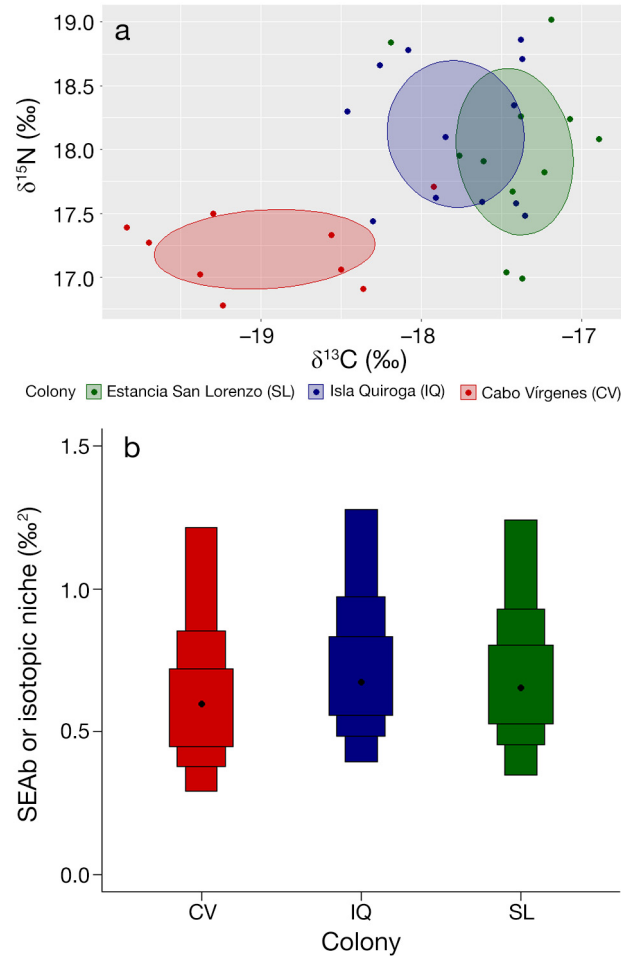


Fig. 3. (a) Magellanic penguin bulk blood isotopic space for carbon and nitrogen and Bayesian standard ellipse area (SEAb; contains about 40% of data, considered the core isotopic niche). (b) SEAb for the 3 studied colonies. Boxes: 95th, 75th and 50th credible intervals; dot: median.

distribution on the Patagonian Shelf. Our results indicate that a large proportion of the adult Magellanic penguin breeding population may remain within, or only slightly north of, the foraging areas used during the breeding season (Sala et al. 2012, Yorio et al. 2021, Blanco et al. 2022). In contrast, only few tracked individuals traveled far north towards

Table 2. Sampled Magellanic penguin colonies, stable isotope values, stable isotope niche metrics, niche overlap between colonies, and main prey contribution in each colony. SEAb: Bayesian standard ellipse area; SEAc: overlap of the isotopic niche; TA: total area in the isotopic space. The Euclidean distance to main prey indicates the contribution of each, the smaller the distance, the larger the contribution of the prey. Colonies: SL: Estancia San Lorenzo; IQ: Isla Quiroga; CV: Cabo Virgenes

Colony	$\delta^{15}\text{N}$ (SD) (‰)	$\delta^{13}\text{C}$ (SD) (‰)	TA (‰ <sup>2</sup> )	SEAb (‰ <sup>2</sup> )	Euclidean distance to:		SEAc Overlap with (%):		
					Anchovy	Sprat	SL	IQ	CV
SL	18.0(0.62)	-17.4(0.35)	1.45	0.76	0.68	2.50	100	34	0
IQ	18.1(0.55)	-17.7(0.41)	1.34	0.78	0.64	2.52	34	100	0
CV	17.2(0.29)	-18.9(0.66)	1.02	0.7	2.17	1.53	0	0	100

Uruguay and Brazil. The large variability in migration distance highlights the importance of the entire Patagonian Shelf for Magellanic penguins breeding along the coast of Argentina.

Given the more pronounced seasonality with shorter breeding season towards the south (Frere et al. 1996), arrival time at the colony is expected to be later in higher latitudes. However, penguins from the southernmost colony in Cabo Vírgenes arrived before penguins in the northernmost colony at San Lorenzo, and mean arrival dates at the central colony on Isla Quiroga was the latest. The differences in arrival dates between colonies might not be the same over years, and local food availability has been shown to be the key driver of timing and ultimately breeding success (Regehr & Rodway 1999, Durant et al. 2003). At IQ, a previous study showed that, if conditions allow, penguins shift their prey during the chick-rearing period from squid to the more energetically valuable sprat (Ciancio et al. 2015, Barrionuevo et al. 2018). The timing of arrival and breeding might thus be optimized to match the higher energy demands during the later period of chick rearing with the peak in local sprat abundance (Sánchez et al. 1995)

During the non-breeding season, tracked individuals from the 3 colonies remained separated within the region of the Patagonian Shelf. During the winter dispersion, individuals generally moved northwards and maintained their position in the latitudinal order of the breeding colonies. Similar dispersion pattern with a restricted movement towards the north have been documented for individuals from other colonies (Yamamoto et al. 2019, Dodino et al. 2021). The northward shift of individuals during winter, and the fact that some individuals from the southern colony remained in the south, highlights the fact that the entire Patagonian Shelf offers suitable conditions for Magellanic penguins across the entire year.

We can only speculate about the reasons why individuals from a genus that is known to have low migration tendency (García-Borboroglu & Boersma 2013), leave the areas of their breeding colony that are then occupied by individuals breeding farther south. A combination of higher temperatures in the north and thus lower energy expenditures during winter (Ciancio et al. 2016), intra-species competition, and movements of prey towards the north (Hansen et al. 2001) might all be interacting drivers. Isotopic analysis provides some evidence that the proportion of anchovy and sprat in the diet remained relatively constant over the year for individuals from SL and CV (Ciancio et al. 2021). During the last period before arrival at the breeding site, individuals from the south-

ern colony had higher amounts of sprat in the diet, compared to penguins from the northern colony where the diet was dominated by anchovy. Isotopic niches of penguins from IQ and SL showed considerable overlap, indicating a change in the diet of IQ penguins, from anchovy during breeding to sprat during the non-breeding period. IQ penguins, instead of migrating southwards to eat sprat (Hansen 1999, Sánchez et al. 1995), move northwards into warmer waters where anchovy are distributed (Hansen et al. 2001). The larger spatial overlap between individuals from the central and northern colonies during the winter, and the more similar oceanographic parameters experienced, might thus be driven by the similarity in their mutual prey preference during winter, indicated by the higher overlap in the trophic niche compared to the individuals from the south.

Speculations exist that Magellanic penguins from Argentina disperse farther north during winter, leaving the Patagonian Shelf (Boersma et al. 2013). Even though our tracking data are limited in terms of populations and time, it seems more likely that they remain within the region of the Shelf during the entire year. This is no real surprise, since the Patagonian Shelf is known to provide good conditions during the winter, providing food for many seabirds (Favero & Rodriguez 2005), penguin species (Pütz et al. 2006), and marine mammals (Falabella et al. 2009). However, the region is also a focus for fisheries and economic development, creating several threats to marine wildlife, including competition for food, the potential to become a victim of by-catch (Crawford et al. 2017), chronic oil pollution (García-Borboroglu et al. 2006), and seismic offshore activities (Pichegru et al. 2017, de Haro et al. 2022). To date, we have not seen a strong effect of these activities on Magellanic penguin populations. However, human activities and the response of wildlife need to be monitored more closely to identify and avoid potential cumulative effects in the future, especially since climatic and ocean changes are believed to affect their prey distribution (Franco et al. 2020). Therefore, we recommend that potential offshore marine protected areas be identified and established within this shelf region, which is of such great importance to marine wildlife in the area.

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