



At-sea distribution, movements and diving behavior of Magellanic penguins reflect small-scale changes in oceanographic conditions around the colony

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Abstract

Penguins are highly specialized divers that are expected to reflect environmental variation by adjusting their foraging behavior. We performed a comprehensive analysis of the at-sea distribution, diving, and foraging performance of Magellanic penguins (*Spheniscus magellanicus*) during the early chick-rearing period over two consecutive breeding seasons. The study was conducted at Cabo dos Bahías, (44° 54' 50" S; 65° 32' 37" W) a breeding colony located south of the latitudinal range of penguins' main prey item Argentine anchovies (*Engraulis anchoita*). We also linked penguin foraging behavior to sea surface temperature (SST) to examine how birds cope with differences in oceanographic conditions. For this, we instrumented 37 adult penguins (18 in 2015 and 19 in 2016) with data loggers. In addition, we recorded chick growth in body mass during the first 12 days of life. Overall, the diving patterns of adult Magellanic penguins were similar in both breeding seasons. However, during 2015, adult breeders spent more time at the sea surface between foraging dives and performed more foraging dives per hour. The time spent foraging was higher in 2016 than in 2015. Foraging penguins also expanded their foraging range more than 100 km during 2016. Temperature records gathered by diving penguins during 2016 showed significantly higher temperatures, both at the sea surface as well as at the bottom of dives. Adults performed a higher foraging effort and chicks gained weight faster during 2016. Site-specific variability in prey distribution and abundance may be responsible for inter-seasonal discrepancies in the foraging and diving patterns. We reasoned that any environmental change could cause a shift in the distribution of anchovies, which would change the foraging behavior of penguins as they attempted to optimize their chick growth. Penguins from Cabo dos Bahías appear to face this environmental challenge with a highly sensitive at-sea foraging performance by increasing foraging effort when necessary.

Keywords Magellanic penguins · Pelagic ecology · Foraging behavior · Sea surface temperature

Introduction

Foraging seabirds are known to respond to temporal and spatial changes in oceanographic features and associated prey availability by employing different feeding strategies, which makes them particularly interesting models with which to study processes and decisions in foraging ecology (Ponchon et al. 2014; Ropert-Coudert et al. 2019; Sutton et al. 2020). Among seabirds, penguins are highly specialized divers which react to oceanic environmental variation (e.g. sea surface temperature (SST) and chlorophyll concentration) (Boersma 2008) as well as prey type and availability (Lescroël and Bost 2005) by adjusting their behavior to exploit resources across all three dimensions of space (Cotté et al. 2007), specifically compensating for local food depletion by increasing their area of foraging or modifying

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search effort (Dehnhard et al. 2015). This explains why penguin species have been proposed as good indicators of ocean health, with ocean change being reflected in their behavior and breeding performance (Croxall et al. 2002; Le Bohec et al. 2008).

The Magellanic penguin (*Spheniscus magellanicus*) breeds along both coasts of South America. The northernmost limit on the Atlantic coast is at 41° S, and on the Pacific coast extends its breeding distribution to 29° S (Boersma et al. 2013). In the Atlantic coast, their colonies are also located in insular areas such as Islas Malvinas (Falkland Islands) and Isla de los Estados, Argentina (Raya Rey et al. 2014). The estimated world population ranges between 2.2 and 3.2 million mature individuals, of which 900,000 breed along the Argentinean coast (BirdLife International 2000), making it the most abundant seabird in Patagonia (Pozzi et al. 2015). On recent decades, population and distributional changes have occurred in the breeding meta-populations of Patagonia Argentina, with some colonies declining, others increasing at high rates and a few newly established colonies (Pozzi et al. 2015). This has led the IUCN (International Union for Conservation of Nature) to consider this species as “Least Concern” (BirdLife International 2000).

Along the coast of Patagonia Argentina, an increase in the number of breeding pairs (by as much as 2.6% per annum) has been recorded in colonies in the north of its distributional range (Schiavini et al. 2005; Pozzi et al. 2015). In contrast, Punta Tombo (the second largest colony in the world) decreased by 22% in the number of breeding pairs between 1987 and 2008 (an annual decrease of approximately 1%), as did other colonies in central Patagonia (Boersma 2008). Sources of these variations have been attributed to favorable environmental conditions in northern Patagonia (added to density-dependent processes), and more erratic and variable conditions in the center of the Magellanic penguin breeding distribution (Pozzi et al. 2015) (see Fig. 1).

The diving and foraging behavior of Magellanic penguins has been widely studied along the Patagonian coast of Argentina with observed variability between colonies being ascribed to local differences in prey availability (Wilson et al. 2005b; Sala et al. 2014). Basically, penguins breeding north of 45° S and south of 50° S prey upon Argentine anchovy (*Engraulis anchoita*) and Patagonian sprat (*Sprattus fuegensis*), respectively (Ciancio et al. 2018). Conversely, birds from colonies located between those latitudes show a broader spectrum of prey species such as other fish (i.e. *Merluccius hubbsi*, *Austroatherina* sp., *Eleginops maclovinus*) and some squid (*Illex* sp. and *Loligo* sp.) (Castillo et al. 2019; Fernandez et al. 2019). Moreover, within the anchovy geographic domain (north of 45°), penguins from the northernmost colonies, forage mainly on juvenile fish, while birds from the southern limit feed mainly on adult fish (Ciancio et al. 2021). The penguin colony of Cabo dos Bahías, (placed

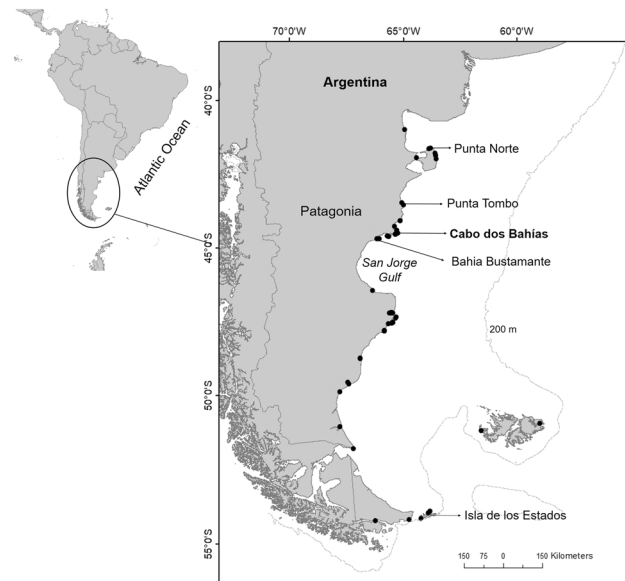


Fig. 1 Distribution of the Magellanic penguin (*Spheniscus magellanicus*) colonies (black dots) along the coast of Patagonia, Argentina. Only the studied colony (Cabo dos Bahías) and others mentioned in the text are named

in the North of San Jorge Gulf) is located at the center of the distributional range of the species in coastal Patagonia, Argentina (Yorio et al. 1998). The surrounding waters of the colony represent the southern limit of the distributional range of the Argentine anchovy, the main prey item of penguins breeding at the northern colonies (Frere et al. 1996; Yorio et al. 2017). The Argentine anchovy extends from 41° to 48°S, but, during late austral spring and early-summer [i.e. the early-chick rearing period of the Magellanic penguins from Cabo dos Bahías (G. Blanco and F. Quintana unpubl. data)], is more abundant between 41° and 45° S, although appreciable inter-annual changes have been observed (Hansen et al. 2001). Such inter-annual variation in prey distribution, potentially derived from oceanographic fluctuations, seems likely to comprise a more variable environmental scenario for penguins provisioning offspring at Cabo dos Bahías. Although the precise drivers of potential prey species abundance are poorly understood, we reasoned that even small-scale changes in oceanographic conditions around Cabo dos Bahías could affect the availability of the main food sources, and this would be reflected in the foraging and diving behavior of penguins breeding at this colony.

Even though the foraging ecology of Magellanic penguins has been relatively well studied (Wilson et al. 2007; Boersma and Rebstock 2009; Rosciano et al. 2018; Fernandez et al. 2019; Ciancio et al. 2021), the high degree of variation (both within and between breeding sites) highlights the need to continue, site-specific and long-term studies at different colonies (Quintana et al. 2021, in press). Here, we performed

a comprehensive analysis of the at-sea distribution, diving and foraging behavior of Magellanic penguins from Cabo dos Bahías during the early chick-rearing period over two consecutive breeding seasons. Additionally, we examined the extent to which penguin foraging behavior might be tied to SST to determine responses to oceanographic features (i.e. SST) in this species. We also aimed to compare our results with those of Magellanic penguins breeding at other colonies, to understand the dynamics and plasticity of their foraging performance.

Methodology

Study area

Field work was conducted during early chick-rearing period, over two consecutive breeding seasons (2015–2016) at Cabo dos Bahías (44° 54' 50" S; 65° 32' 37" W, Fig. 1), located at the north limit of the San Jorge Gulf. This colony hosts approximately 12,000 breeding pairs spread over an area of 22 ha (Capurro et al. 1988; Pozzi et al. 2015). A few counts suggested that there have been no variation in the number of breeding pairs over 15 years, indicating population stability (Pozzi et al. 2015), although the most recent counts suggest that the number of breeding pairs have decreased at approximately 7% per annum since the last record in 2010 (G. Blanco and F. Quintana unpub. data).

Deployment of animal-attached devices

Data loggers were deployed on adult penguins ($N=37$) during the early chick-rearing period. In 2015, between December 7th and 13th, 18 birds were instrumented (seven females, eight males and three birds of unknown sex). In 2016, between December 9th and 13th, 19 birds (11 females, four males, and four of unknown sex) were instrumented. Sex was determined using morphometric measurements following Bertellotti et al. (2002). Penguins were equipped with either an Axy-trek® (three birds in 2015 and nine in 2016), which incorporates a GPS, accelerometer (records not included in this study), depth (i.e. pressure) and temperature sensors (www.technosmart.eu), or a Gipsy-4® (GPS only), together with a small Axy-Depth® including temperature and depth recorders (25 birds) (www.technosmart.eu). All devices were programmed to collect positional data at 1 Hz sampling frequency (increasing the accuracy of locations to 2 m) and 8-bit resolution (Axy trek® Manual). Temperature resolution was 0.1 °C (range −20 to +60 °C) and depth (i.e. pressure) resolution was 20 mbar. We used the records of water temperature to derive in situ surface and bottom temperatures. To avoid delays that may occur in temperature sensor response times (Sala et al. 2017), we computed

the surface temperature by considering mean temperature records at depths between 2.5 and 5 m of each dive. We considered that the bottom temperature corresponded to the mean temperature of the bottom phase of each foraging dive (Sala et al. 2017).

We monitored nests daily recording the presence of adults. In general, the individual that was present in the nest during two consecutive surveys, was promptly to start a foraging trip. Those animals were selected for deployment to avoid logger's battery consumption when penguins were still in the nest. We gently removed the penguins from their nest and attached the loggers to their lower back following Wilson et al. (1997). Loggers were attached using 4 strips of tesa tape® 4651. We first place the tape under the feathers with the glue facing up, then place the logger and wrapped the tape around it. Finally, one last piece of tape was placed over the device to cover the unions of the strips of the tape.

The instrumentation procedure lasted less than ten minutes and birds were returned to their nest after deployment. We removed all data-loggers after a single foraging trip (range 7–74 h). In addition, we monitored all nests of equipped animals every three to five days until the end of December (late chick rearing period) to ascertain that all nests continued to breed normally.

Dive analysis

Diving behavior was analyzed using the software MTDIVE (Jensen Software System), designed to classify the phases of a complete dive (descent, bottom, and ascent phase). A dive was considered as every submersion deeper than 1.5 m following previous analysis performed on the same species (Sala et al. 2012b). We classified foraging and non-foraging dives by calculating the frequency distribution of maximum dive depths and the total time spent at the bottom per dive. Based on the bimodal distribution in maximum dive depth for both seasons, we considered as foraging dives only those with bottom durations longer than 2 s and to depths greater than 16 and 14 m for 2015 and 2016, respectively [see Sala et al. (2014)]. Even though in some cases penguins could predate at shallower depths, recent studies showed that, in Cabo dos Bahías, captures in the first meters of the water column occurred in less than 3% of the dives (Del Caño et al. 2021).

We thus obtained both the total number of dives and the number of foraging dives per trip. Dive depth (m), dive duration (s), post-dive interval (s) (recovery time between consecutive foraging dives), total time diving (h) and total time foraging (h) (defined as the summed duration of foraging dives) were calculated. We also obtained the time invested in the descent, bottom and ascent phases (s) of each dive for every foraging trip (Simeone and Wilson 2003; Bost et al. 2007; Sala et al. 2014). We defined diving effort as the ratio

between dive duration and dive cycle duration (dive duration + post-dive interval). The diving rate was calculated as the number of foraging dives per hour [modified from Raya Rey et al. (2012), Sala et al. (2014)].

Spatial analysis and foraging trip variables

We mapped and analyzed the trajectories of all individuals using ArcGIS 9.3. When we used two different devices on a single bird (Gipsy-4® (GPS only), + Axy-Depth®, see “Deployment of animal-attached devices”), information (i.e. location and dive data) from both sources had to be merged by matching times and, therefore, each location was assigned to a particular dive. As a result, at-sea locations were also classified as non-foraging or foraging locations following the depth-duration diving threshold above mentioned.

We calculated trip duration as the elapsed time between the first and the last location in the water, even if tracks were incomplete because the logger did not record the majority of the inbound track, when possible, time of the last location in the water before going back to the nest was retrieved. Other foraging trip variables such as; maximum distance to colony (km) (distance between the location of the nest and the farthest point of the track), total distance traveled (km, calculated by adding the distance between consecutive locations for the complete track), and track sinuosity (obtained from dividing maximum distance to the colony by the total distance traveled (Weimerskirch et al. 2002) were also calculated. Using the outbound tracks of birds, we calculated a linear directional mean to describe the mean direction of the birds heading to the foraging areas. To compare individual variations in area

used, we defined the total foraging range by calculating Minimum Convex Polygons (MCP) for each individual, including all locations associated to foraging dives and the total range by calculating MCP that included all locations for each individual (modified from Pichegru et al. (2013)). We also performed a fixed Kernel Density Analysis (Worton 1989) using Hawth's tools for ArcGIS 9.3 (Beyer 2004) with a smoothing factor $h = 1000$ m, to compare foraging areas between the two years of study as it estimates the probability densities for the season. We estimated Kernel contours using foraging locations for both years (90, 50 and 25% Utilization Distribution Areas). In addition, the bathymetry of the areas in which the animals were foraging was calculated by overlapping the foraging locations with a bathymetry map generated for the study area (Sanchez Carnero, pers. com., see Fig. 2). We also overlapped spatially and temporarily, all foraging locations with SST for the study area. SST images were obtained from MODIS (<https://oceancolor.gsfc.nasa.gov>) at 1 km spatial resolution. The presence of clouds during days when animals were tracked, had at some specific locations clouds that inhibited the use of satellite images to each specific day. Therefore, we derived weekly composites to overlap the time in which animals travelled during each studied season. As such, we assigned a SST value to each location to calculate SST experienced by individuals. In addition, we calculated overall mean SST of the study area to compare overall variation in SST between years.

We analyzed all spatial variables using ArcGIS 9.3, extensions: data management, spatial statistics, and spatial analyst tools.

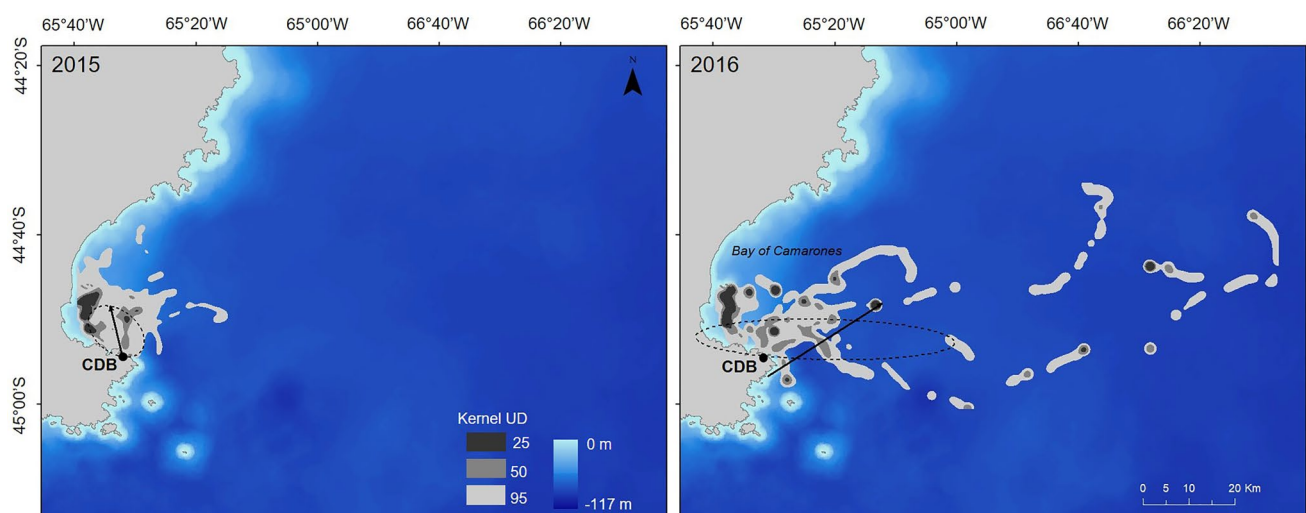


Fig. 2 Foraging areas of Magellanic penguins breeding at Cabo dos Bahías (CDB) during two consecutive breeding seasons (2015, 2016) represented by Kernel contours. Black arrow represents outbound

directional mean, dashed polygon represent its standard deviation. Blue shades represent the bathymetry

Nest monitoring and chick growth

At the beginning of the breeding season, nests were marked and monitored weekly. Once the eggs hatched, nests were revisited daily. Chicks were marked using a livestock crayon indicating hatching order. Body mass was recorded every 3–5 days, using a 100 g, 300 g, 600 g, or 1000 g spring scale (Barrionuevo 2015; Giudici et al. 2017). We selected for this analysis, all chicks from instrumented nests and chicks that hatched within the same week of those chicks from experimental nests (58 and 35 nests, for 2015 and 2016, respectively).

Statistical analysis

Since there were no differences between spatial and diving parameters (e.g. total number of dives, number of foraging dives, total time of foraging dives, dive rate, trip duration, total distance traveled, maximum distance to colony, sinuosity, MCP) between sexes, data from females and males were pooled (*t* test, Mann–Whitney *U* tests all $p > 0.05$).

To analyze differences between years, we compared all spatial variables and those diving variables for which we obtained a unique value per individual (e.g. total number of dives, number of foraging dives, total time diving, total time foraging, and dive rate), using *t* tests or Mann–Whitney *U* tests depending on normality of data (Zar 1999).

General mixed effects models (GLMM) fitted by maximum likelihood (ML) were used to test differences between years for those diving variables with more than one value per individual (e.g. dive depth, dive duration, post-dive interval, decent, bottom, and ascent duration, diving effort). For these analyses, year was included as a fixed factor and bird identity as a random factor to account for potential pseudoreplication (Crawley 2007; Zuur et al. 2009). Additionally, for those parameters with several measurements per animal we obtained a mean value per parameter per individual. Then we used these mean values to calculate a grand mean per year, the standard deviation, and its range.

Because maximum dive depth has an important effect on dive duration, post-dive interval, descent, bottom and ascent duration; the analysis of these variables included the effect of dive depth as covariate (Tremblay and Cherel 2000). To deal with non-Gaussian distributions, we used GLMMs with poisson errors and log-link function corrected for over dispersion (Crawley 2007).

Non-Linear Mixed Models (NLMM) were used to evaluate differences between years in early chick growth in body mass (until 12 days of age) (Pinheiro and Bates 2000). Body mass was fitted to a linear equation where y_t is chick mass at age t , and a and b , are the growth rate and the intercept, respectively. This equation has been shown to fit early chick growth of Magellanic penguins adequately (Barrionuevo

2015). Breeding season was included as predictor variable. Because chick growth may depend on hatching order and brood size (Barrionuevo et al. 2018), we also included rearing conditions (i.e. combination of the hatching order (O) and brood size (BS) at 12 days) as predictor variable. Growth parameters (a and b) were modeled by predictor variables. Growth parameters and chick identity nested on nest identity were included as random effects.

GLMMs were run using the function *lmer* from the package *lme4*. For the NLMM we used the function *nlme* from the package *nlme*. We compared the models with and without the eliminated variables with the function *anova* using the Chi-square test goodness of fit (χ^2 parameter) for GLMM and the likelihood ratio test (L-ratio) for NLMM. All statistical analyses were performed using open-source statistical package R version 3.6.1 (R Development Core Team 2019) with a level of significance of $p < 0.05$. Results are shown as mean $\pm$ standard deviation (SD).

Results

We recorded dive information of one complete foraging trip from 34 of 37 instrumented individuals, consisting of 21,694 dives (two loggers did not record information and one recorded a partial trip). The GPS units (both those on Axy-trek and Gipsy 4) recorded 22 complete foraging trips (13 GPS recorded incomplete tracks mostly due to failure to record the inbound trajectory).

Diving and foraging behavior

Departures to the sea occurred all day, being slightly higher at late afternoon (departure local times: 00:00–06:00 = 16.7%, 06:00–12:00 = 20%, 12:00–18:00 = 23.3%, 18:00–00:00 = 40%). Arrival local time to the colony also took place across the 24 h cycle with a maximum in the early afternoon (0:00–06:00 = 10%, 06:00–12:00 = 20%, 12:00–18:00 = 43.3%, 18:00–00:00 = 26.7%).

Overall, the diving pattern of adult Magellanic penguins was similar for both breeding seasons (Table 1). However, during 2015, adult breeders spent more time at the sea surface between foraging dives (35.2 ± 8.8 vs. 32.7 ± 9.3 s; GLMM, $\chi^2(1) = 7.202$, $p < 0.0072$; Table 1) and performed more foraging dives per hour (37.1 ± 6.3 vs. 31.0 ± 5.0 ; *t* test = 3.05, $p = 0.0047$; Table 1). The time foraging was higher in 2016 than in 2015 (11.2 ± 5.0 vs. 7.1 ± 2.8 h; *t* test = 2.90, $p = 0.007$; Table 1). The maximum dive depth recorded was 89.3 m although adult breeders generally foraged at depths ranging from 20 to 60 m. Maximum dive duration recorded was 251 s (4.2 min), while mean foraging dive duration ranged between 79 and 147 s. Foraging dives mainly occurred during daylight hours (05:00–21:20 h at the

Table 1 Diving behavior, at-sea movements and oceanographic features of the areas used by Magellanic penguins (*Spheniscus magellanicus*) breeding at Cabo dos Bahías during two consecutive breeding seasons (2015–2016) during the early chick-rearing period

Dives	N (birds)	2015		2016		p value
		Mean $\pm$ SD	Range	Mean $\pm$ SD	Range	
Total no. of dives (n)	34	589 $\pm$ 185	330–942	682 $\pm$ 504	99–2159	0.73
Trip duration (h)	30	23.3 $\pm$ 7.2	10.3–36.0	30.4 $\pm$ 16.7	7.0–74.3	0.13
No. of foraging dives (n)	34	258 $\pm$ 104	69–411	342 $\pm$ 160	74–788	0.11
Percentage of foraging dives (%)	34	49 $\pm$ 17	18–67	59 $\pm$ 19	24–91	0.11
Dive depth (m)	35	36.1 $\pm$ 8.3	22.9–59.8	41.8 $\pm$ 11.6	20.3–60.3	0.15
Dive duration (s)	35	103.9 $\pm$ 19.5	79.2–147.0	115.69	88.0–137.9	0.13
Post-dive interval (s)**	35	35.2 $\pm$ 8.8	26.9–43.0	32.7 $\pm$ 9.3	26.13–39.36	0.0072
Total time diving (h)	33	11.0 $\pm$ 2.8	7.7–16.6	19.0 $\pm$ 15.1	2.6–68.6	0.05
Total time of foraging dives (h) **	33	7.1 $\pm$ 2.8	3.3–13.0	11.2 $\pm$ 5.0	2.4–20.1	0.007
Descent phase (s)	35	30.3 $\pm$ 8.2	18.3–51.2	35.3 $\pm$ 5.8	21.7–41.0	0.15
Bottom time (s)	35	40.1 $\pm$ 7.7	24.5–56.5	43.4 $\pm$ 7.2	28.0–61.1	0.28
Ascent phase (s)	35	31.6 $\pm$ 13.4	2–102	37.3 $\pm$ 37.3	1–113	0.16
Diving effort	35	0.8 $\pm$ 0.04	0.7–0.8	0.8 $\pm$ 0.05	0.7–0.9	0.16
Dive rate (foraging dives h ⁻¹)**	33	37.1 $\pm$ 6.3	26.3–46.1	31.0 $\pm$ 5.0	19.9–40.9	0.0047
At sea movements						
Max. distance to colony (km)	23	17.6 $\pm$ 4.4	11.5–24.8	39.3 $\pm$ 35.9	7.9–113.4	0.16
Total distance traveled (km)	22	76.1 $\pm$ 23.9	38.3–111.2	142.8 $\pm$ 95.1	24.7–335.4	0.05
Sinuosity of the foraging path	21	0.2 $\pm$ 0.0	0.2–0.3	0.2 $\pm$ 0.1	0.2–0.3	0.93
Foraging range (MCP, km ²)	22	82.3 $\pm$ 73.8	13.9–273.4	493.2 $\pm$ 772.6	4.0–2291.2	0.09
Total range (MCP, km ²)	24	103.1 $\pm$ 85.4	16.6–321.6	544.4 $\pm$ 783.7	9.1–2491.4	0.08
Oceanic features						
Mean temperature at bottom of dive**	35	11.7 $\pm$ 0.53	10.3–12.4	12.3 $\pm$ 0.5	11.6–13.4	0.0001
Temperature at surface**	35	12.7 $\pm$ 0.5	12.4–13.3	13.5 $\pm$ 0.4	13.0–14.2	0.007

Bold values indicate statistical significance

All dive statistics referred to foraging dives (see text)

**Statistical differences between years of study

study area during the study period) with almost no foraging dives during dark hours (just 2%).

Use of marine areas, at sea movements and foraging parameters

During the early chick-rearing period 2015, penguins from Cabo dos Bahías headed north-northwest (outbound mean direction 346.2°) on the way to their foraging areas. Post travelling, these individuals foraged inside Camarones' Bay (Fig. 2a). During the following season, penguins moved northeast (outbound mean direction 57.5°) but expanded the foraging areas outside the Camarones' Bay by more than 100 km to the East (Fig. 2b) although there were no statistical differences between seasons (Table 1, Fig. 2b). The apparent variation in the foraging range between seasons was primarily due to a particular individual that exploited an extensive area of 2,291 km² (Fig. 2b). Overall, we found no significant difference in any of the characteristics of foraging trips between seasons (Table 1), even after considering

the particular foraging pattern of one of the instrumented penguin. Only the total distance travelled appeared slightly higher during 2016 (Kruskal–Wallis test, $df = 1$, $\chi^2(1) = 3.88$, $p = 0.05$, Table 1), but this slight difference could have been driven by that one individual during 2016. In general, foraging trips lasted approximately one day covering average maximum distance of approximately 100 km during which time the penguins reached a maximum average distance from the colony of 23.5 km (range: 7.9–113.4 km) (Table 1).

The use of the foraging areas differed between years (Fig. 2). During 2015, penguins foraged in a more localized area than during 2016. The total area used to forage in 2015 (represented by 95% UD) was 300.5 km² and was significantly smaller than that of 2016 (i.e. 675.3 km²). The foraging areas of both seasons overlapped almost exclusively inside Camarones Bay (187.5 km²) where 62% of the area used during 2015 was also exploited during 2016 breeding season. Interestingly 25% core area (22 km² in 2015 and 38 km² in 2016) also showed an overlap of 12 km² inside the bay.

Oceanographic features

Penguins foraging during 2015 explored shallower waters than those in 2016. The mean depth of 2015 foraging areas was 36.7 ± 14.4 m, while the area used by penguins during 2016 was 59.3 ± 21.6 m (Fig. 2). In addition, during 2016, penguins foraged over warmer waters than those for 2015. Temperature records gathered by diving penguins during 2016 showed significantly higher values of temperatures both at surface (GLMM, $\chi^2(1) = 7.264$, $p < 0.007$; Table 1) as well as bottom dive depths (GLMM, $\chi^2(1) = 14.19$, $p < 0.0001$; Table 1). In agreement with the penguins' tag data, the mean SST obtained from overlapping individual locations with satellite images was also higher in 2016 than in 2015 (12.2 ± 0.4 °C in 2015 and 13.1 ± 0.4 °C in 2016, Fig. 3a). The SST across the whole study area varied as much as 3–4 °C between years (Fig. 3b).

Early chick growth

During 2016, chicks gain mass at a higher absolute rate, as year was the significant variable that affected ordinate at the origin (b) and growth rate (a) (NLMM; a: L-ratio = 108.53, $p < 0.0001$; b: L-ratio = 18.72,

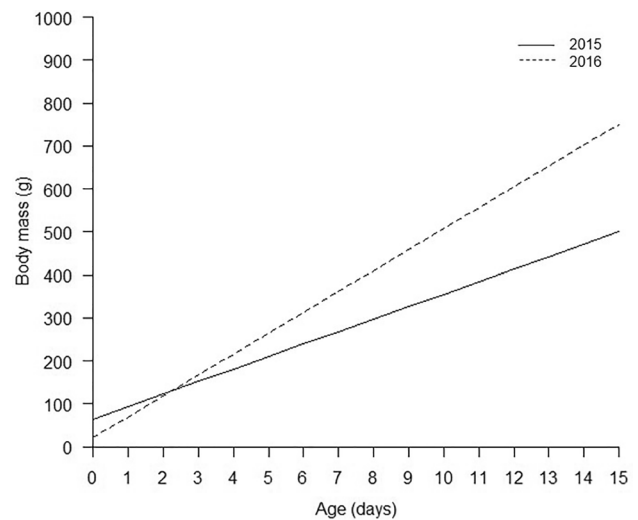


Fig. 4 Early chick growth (in body mass) during the first 12 days of age of 58 nests in 2015 and 36 in 2016. All measurements corresponded to nests of instrumented adults or to nests in which chicks hatched at the same dates of those nests with instrumented adults. Growth data were fitted to polynomial equation

$p < 0.0001$; Fig. 4), while the rearing conditions only affected the growth rate (NLMM; a: L-ratio = 240.93, $p < 0.001$; b: L-ratio = 2.59, $p = 0.45$).

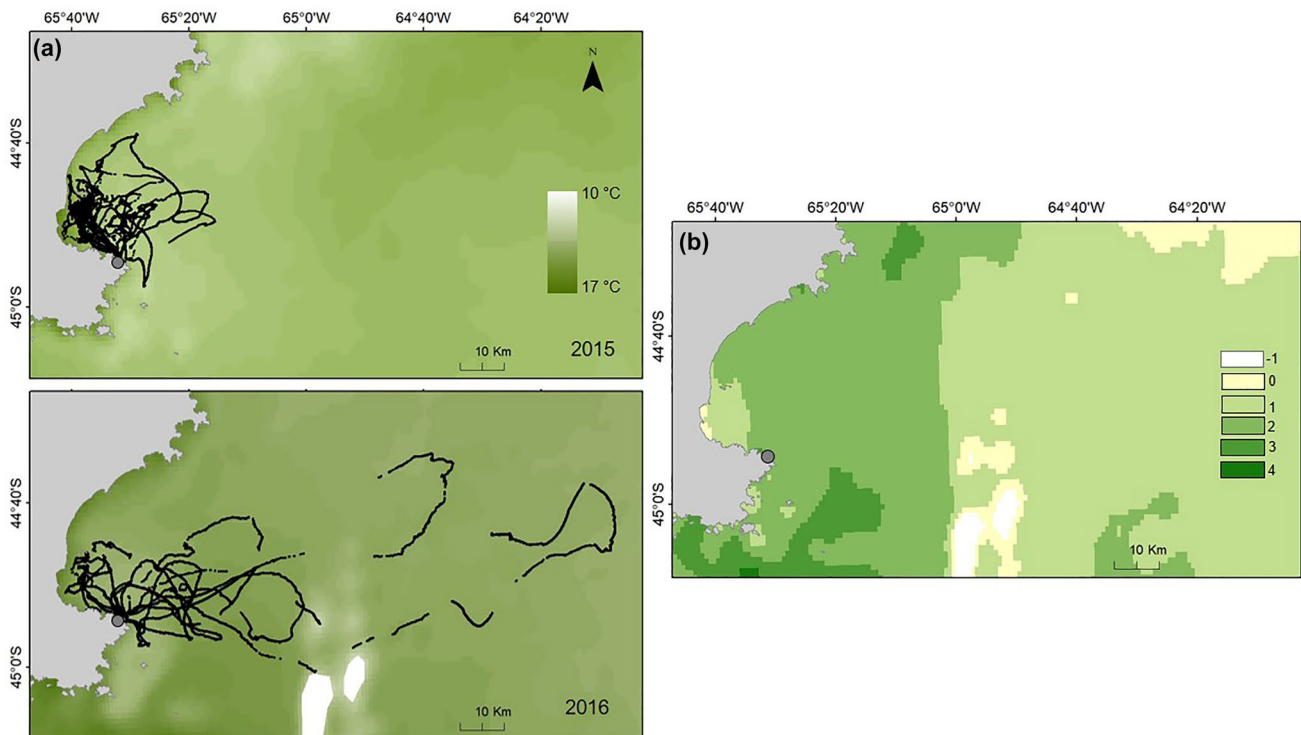


Fig. 3 **a** Mean satellite derived SST for the study area for December 7–13th in 2015 and 2016. Black dots represent foraging Magellanic Penguin tracks. **b** Differences in SST in the study area calculated by

subtracting values from 2015 to 2016 SST. Scale represents difference in °C. White spots indicate no data

Discussion

In this study, we described for the first time the foraging behavior of Magellanic penguins from Cabo dos Bahías during consecutive years with different thermal conditions. Cabo dos Bahías is located south of the latitudinal range of the penguins' main prey, the anchovy (Frere et al. 1996; Hansen et al. 2001). The abundance of this pelagic school fish can vary considerably during the chick-rearing phase in the vicinities of the Magellanic penguins colonies located in the center of their breeding distributional range, along the Patagonian coast of Argentina, as the fish population effectively expands into, and out of, its distributional limits (Wilson et al. 2011). Such site-specific variability in prey distribution and abundance can result in corresponding inter-seasonal variation in the foraging and diving patterns of the Magellanic penguin. We reasoned that even slight environmental change could cause a shift in the distribution of anchovies forcing penguins from Cabo dos Bahías to adapt their foraging behavior to provision their chicks most effectively. We believe that the small environmental variations made apparent by our study are behind the subtle changes in the foraging and diving of the penguins that we observed during the early chick-rearing period. Previous studies have shown that this species has remarkable plasticity in the face of environmental change, adjusting its foraging and diving behavior in response to heterogeneity of marine productivity (Wilson et al. 2005a; Boersma and Rebstock 2009; Sala et al. 2012a, 2014; Gómez-Laich et al. 2015). Our results add another study case and area to this framework, explaining, at least in part, the distributional and at-sea behavioral changes that this species is exhibiting (Gómez-Laich et al. 2015).

Diving behavior

Although we did not perform any diet evaluation during the study period, it is reasonable to assume that Magellanic penguins during the chick-rearing periods of 2015 and 2016 were foraging on similar prey items. Birds in the north of the latitudinal range mainly consume anchovy (Ciancio et al. 2018; Fernandez et al. 2019) and diet studies at neighboring colonies, all located ~45° S, show that anchovy is the main prey item delivered to chicks during early chick-rearing period (Yorio et al. 2017; Ciancio et al. 2018), with other fish species and squid occurring at lower frequencies (Castillo et al. 2019). Moreover, our data showed that birds from Cabo dos Bahías are acquiring their prey at depths ~40 m which accords with the vertical distribution of anchovies at this time of the year (i.e. 20–40 m) (Hansen et al. 2001; Pájaro et al. 2005).

During 2015, penguins performed more dives per unit time at sea (dive rate, foraging dives h^{-1}), and spent more time at the surface recovering oxygen between dives (post dive duration), but the total time invested in foraging dives was higher in 2016. Sala et al. (2012b) described how penguins from colonies where prey acquisition was more profitable (a higher incidence of prey ingestion per unit time), spent less time underwater, indicating that the variation in prey size and prey encounter rate can be compensated by increasing the total time diving. In fish-eating penguins, prey capture involves high energy expenditure as birds will pursuit prey by increasing their swimming speed, so that oxygen reserves are used faster (Wilson et al. 2002), curtailing (depth-dependent (Peters et al. 1998)) dive duration. As a result penguins facing high prey availability will invest overall less time underwater. Conversely, long dives are likely to be indicative of birds using minimized power as they search the water column for prey. Variation in foraging behavior of diving birds has been attributed to differences in prey availability and prey items (i.e. prey size) (Elliott et al. 2008). For example, strong yearly differences in foraging behavior of Magellanic penguin from a Beagle Channel colony (54° 53' S; 67° 34' W) have been explained by changes in food availability near the breeding grounds (Scioscia et al. 2016). Similarly, Wilson et al. (2005a, b) modelled how Magellanic penguins adjust their at-sea behavior to prey movements to maximize foraging performance. They showed that when prey abundance is low, penguins must spend more time underwater to increase the overall probability of finding prey by effectively increasing search effort. To do that, birds may increase their total (and proportionate) time underwater and, as a consequence, reduce the number of foraging dives per unit time (Sala et al. 2014). This was also concluded for Magellanic penguins breeding in southern colonies of costal Patagonia where a greater diving effort was observed as the main prey decreased (Scioscia et al. 2016).

Although, anchovy is present within the foraging range of penguins from Cabo dos Bahías, during the chick provisioning period (early December), anchovy spawning adults tend to move north of 45° S where reproduction occurs (Ehrlich et al. 2000; Hansen et al. 2001). In addition, anchovy distribution correlates tightly with thermal fronts, and it has been suggested that there is appreciable variability in the inter-annual position of thermal fronts at latitudes relevant for our study (Romero et al. 2006; Glembocki et al. 2015). Changes in the temperature of the water column but mainly in SST between seasons, recorded by both our tags and satellite imagery could have influenced the distribution of the main prey of penguins and explain the variability observed in the foraging behavior of birds from this colony. A greater foraging effort during the warmer late spring of 2016 could have

also generated the observed increase (although not significant) in the foraging trip duration during 2016. Inter-annual comparison of the at sea behavior of foraging penguins from this particular colony suggests an apparently more efficient foraging performance during 2015. Thus, we may suggest that animals had to increase their effort to acquire food during 2016.

Our analyses of chick growth, showed inter-seasonal differences in early growth rate. Chicks from 1 to 12 days old gained weight faster during 2016 than in 2015 breeding season, seemingly at odds with the foraging effort. This brings in to question the precise mechanisms by which birds locate prey and ultimately reduce movement away from the colony as a function of prey density. Being central place foragers, penguins move radially out from their colonies travelling presumably to move rapidly through the colony-dependent prey-depleted area (Ashmole's HaloFurness and Birkhead 1984; Birt et al. 1987)). As birds travel out, they engage in V-shaped dives of variable depth, which is considered to be an effective way of sampling the water column for prey before adopting U-shaped dives at sites where they actively forage. Optimal foraging theory (Krebs et al. 1983; Parker and Smith 1990) predicts that central place foragers should reduce radial travel to optimize the net rate of energy uptake (Andersson 1978; Bovet and Benhamou 1991; Cresswell et al. 2000; Dornhaus et al. 2006). But an appreciable problem is that animals often cannot know about the availability of resources in places farther away; sites where they have not visited. We propose that, in this instance, the conditions for active foraging in 2016 were inadequate for it to take place in the areas exploited by birds in 2015, relatively close to the colony. Instead, birds travelled further, and in so doing, encountered relatively greater prey densities than in 2015, which ultimately led to better provisioning of chicks in 2016 than 2015.

At sea movements and foraging distribution

Penguins were consistent with the heading to the foraging grounds within seasons. However, inter-annual differences between travel directions during the outbound phases of the foraging trips were notable. Such differences are expected as seabirds foraging areas may change frequently in relation to the ocean characteristics that drive prey distribution (Bonadonna et al. 2003). The direction of the path followed by penguins may be related to predictability of resources. For instance, in colonies where prey distribution is stable, penguins appear to follow the same movement patterns over years (Raya Rey et al. 2010; Sala et al. 2012a; Wilson et al. 2015). A clear example of heading and location consistency of the foraging areas has been documented for Magellanic penguins from Punta Norte, San Lorenzo, colony at Península Valdes (42° 04' S; 63° 49' W) for more than 10 years

(Quintana and Wilson unpub. data). At this colony, located at the northern limit of the anchovy distribution, penguins are exposed to a clear and stable environmentally driven scenario of prey availability (Sala et al. 2014; Gómez-Laich et al. 2015). Accordingly, this colony became the most abundant along the Patagonian coast (García Borboroglu et al. 2019), increasing at an annual rate of 1.2% (Pozzi et al. 2010). The fact that birds from Cabo dos Bahías changed their outbound directions between their two consecutive breeding seasons may indicate that resources in the north of the San Jorge gulf may become less profitable, inciting penguins to adapt to these conditions through flexible foraging behavior. We also note that heading to the foraging areas during 2016 was more variable which also supports the idea of low predictability of prey during that season. Moreover, although the foraging areas for both seasons overlapped to some degree, during 2016, penguins considerably extended the area covered to forage, up to the double that of 2015. This points to the importance of Camarones Bay as a key marine indicator sector for foraging penguins from Cabo dos Bahías. The overlap between seasons occurred almost exclusively in this bay, also highlighting the importance of this coastal area for the adult breeders of this colony.

The Patagonian shelf is characterized by strong tidal regimes and intense offshore winds (Palma et al. 2004), which have a direct effect on the areas used by penguins from Cabo dos Bahías to forage. As such, tidal mixing produces sharp gradients between vertically homogeneous coastal waters and mid-shelf stratified waters, generating tidal fronts. Although a near coastal chlorophyll-a bloom develops between 45° S and 52° S in the summer, some areas along this region have marked inter-annual variability (Romero et al. 2006). Even if the location of fronts are stable, their intensity could vary depending on the variation of wind and heat flux. For example, westerly winds in Camarones Bay are very intense and persistent averaging 7.8 m s^{-1} (Labraga 1994), and reversal velocities with maxima that exceeded 1 m s^{-1} associated with tidal currents were registered (Pisoni et al. unpub. data). Thus, animals breeding at Cabo dos Bahías are exposed to oceanographic features where the proximity of frontal areas would seem to increase their probability of finding food, but the mentioned variability of the region may decrease the overall predictability of the resources.

Environmental data such as SST is known to provide valuable insights on how the distribution of primary productivity drives the distribution of predators. Indeed, even small changes in SST can cause large changes in fish distribution (Roy et al. 2007; Silva et al. 2016). Our results demonstrate that SST at the study area can vary by almost 1 °C between years. Moreover, in some sections of the study area, SST was 3–4 °C higher in 2016 (see Fig. 3). Anchovy is generally found in temperatures ranging from 8 to 16 °C, but it

is particularly strongly associated with waters between 10.5 and 13.5 °C (Hansen et al. 2001; Sala et al. 2017). Although penguins at Cabo dos Bahías foraged in waters within this temperature range, when birds experienced temperatures closer to the higher end of the range (13 °C), they could be increasing their foraging effort. Therefore, this variability in SST and the subsequent change in foraging effort during 2016 could have been driven by the inter-annual differences in SST in the study area. These findings accord with observations on Magellanic penguins at the north end of this species' distribution, which increase foraging effort when they experience high SST (Sala et al. 2017).

Barriónuevo et al. (2018) suggested that only extreme SST variations could be an indirect indicator of breeding performance in the Magellanic penguin; the lower the SST, the higher the growth rate of chicks, indicative of enhanced foraging performance. However, small changes in SST did not appear to be a good indicator of breeding performance; this could be the case of penguins from Cabo dos Bahías as the SST variation between years was compensated by increasing foraging effort achieving a better growth rate of chicks when temperature was higher (but still within the range of their preferred prey). We note that SST has been described as an indirect predictor of penguin distribution, breeding success, mass at fledging, and timing of egg laying (among other variables) in several penguin species around the world (Guinet et al. 1997; Cullen et al. 2009; Boersma and Rebstock 2014; Karnauskas et al. 2015; Carroll et al. 2016).

Comparison with other colonies

Penguins from Cabo dos Bahías travel very short distances to find their food (~ 24 km) when compared to other colonies along coastal Patagonia (Boersma and Rebstock 2009; Gómez-Laich et al. 2015; Rosciano et al. 2018). However, they spend considerable amount of time at sea and move greater distances within the foraging areas (~ 100 km). Additionally, the sinuosity of the tracks demonstrated a high proportion of loop-shaped trips (see Rosciano et al. (2018)). In colonies located north of Cabo dos Bahías (i.e. Punta Norte/San Lorenzo), penguins travel longer distances to reach feeding grounds, but spend less time within the foraging area. On the contrary, penguins from Bahía Bustamante (80 km south from Cabo dos Bahías) invest a greater amount of time in the foraging trips (~ 38 h) (Sala et al. 2012a) than penguins from Cabo dos Bahías. The total time that animals spend in the foraging area may be an indication of prey acquisition; implying that birds in areas with high prey availability would complete their energetic demands in shorter periods. Therefore, in areas with low resources, penguins would take longer finding

food for them and their chicks to the same extent that was observed at this colony during the period of this study.

Another indication of differences in prey availability may be explained by the percentage of foraging dives performed in one trip: while penguins from Cabo dos Bahías foraged on average during 54% of their dives, the foraging dives of penguins from colonies located in north Patagonia constitute 82% of their total dives (Sala et al. 2014; Gómez-Laich et al. 2015). By contrast, at colonies located within the same distributional range as Cabo dos Bahías, this percentage is lower than 40% (Sala et al. 2014). Additionally, another source of this variation could be explained on the fact that individuals from northern colonies may be preying upon juvenile fish while colonies surrounding Cabo dos Bahías prey on adult fish (Ciancio et al. 2021). Although fish recruits tend to be more sensitive to changes in the environment, the areas where penguins are foraging upon this age class seem to be more stable as high productivity areas (i.e. Valdés front) are influenced by the bathymetry (Pisoni et al. 2015).

Overall, although based on two years of study, our results suggested that this population might be adjusting its behavior to variability of local environmental conditions because foraging behavior reflected unpredictability of resources within the foraging range of Magellanic penguins breeding at Cabo dos Bahías. Continuation of this research complemented with population monitoring and studies describing penguins' diet throughout the years (e.g. stable isotopes or metabarcoding), would help to elucidate if modifications in the long-term oceanographic conditions that are taking place in this area, will be mirrored in the behavior and survival of these colonies.

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Author contributions GSB and FQ conceived the study. GSB, GM, GD-O, and FQ collected data. JPP analyzed oceanographic data. GSB analyzed spatial data. NAG analyze dive data. LG completed statistical analysis. GSB and FQ wrote the initial manuscript. GD-O provided resources. All authors contributed to the reviewing and editing.

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Availability of data and material The datasets generated and analyzed during this study are available from the corresponding author on request.

Declarations

Conflict of interest All authors declare that they have no conflict of interest.

Compliance with ethical standards Research permits (No. 075-Ss-CyAP/15 and 133-SsCyAP/16) were granted by *Subsecretaría de Turismo y Areas Protegidas* and *Dirección de Fauna y Flora Silvestre*, dependent from the Ministry of Tourism and Protected Areas of Chubut Province, Argentina. Handling of penguins during instrumentation was performed as efficiently as possible.

Informed consent We confirm that the manuscript has been read and approved by all named authors.

References

- Andersson M (1978) Optimal foraging area: size and allocation of search effort. *Theor Popul Biol* 13:397–409
- Barriónuevo M (2015) Inversión parental en el Pingüino de Magallanes (*Spheniscus magellanicus*): asincronía de eclosión, causas próximas y últimas
- Barriónuevo M, Ciancio J, Marchisio N, Frere E (2018) Parental body condition and high energy value of fish determine nestling success in Magellanic penguin (*Spheniscus magellanicus*). *Mar Biol* 165:1–16
- Bertellotti M, Tella JL, Godoy JA, Blanco G, Forero MG, Donazar JA, Ceballos O (2002) Determining sex of Magellanic Penguins using molecular procedures and discriminant functions. *Waterbirds* 25:479–484
- Beyer HL (2004) Hawth's Analysis Tools for ArcGIS. Available at <http://www.spatialecology.com/htools>
- BirdLife International (2000) *Spheniscus magellanicus*. The IUCN Red List of Threatened Species 2020. eT22697822A157428850 <https://doi.org/10.2305/IUCN2020-3RLTST22697822A157428850en> Downloaded on 19 May 2021
- Birt V, Birt T, Goulet D, Cairns D, Montevecchi W (1987) Ashmole's halo: direct evidence for prey depletion by a seabird. *Mar Ecol Prog Ser* 40:205–208
- Boersma PD (2008) Penguins as marine sentinels. *Bioscience* 58:597–607
- Boersma PD, Rebstock GA (2009) Foraging distance affects reproductive success in Magellanic penguins. *Mar Ecol Prog Ser* 375:263–275
- Boersma PD, Rebstock GA (2014) Climate change increases reproductive failure in Magellanic penguins. *PLoS ONE* 9:e85602
- Boersma PD, Frere E, Kane O, Pozzi LM, Pütz K, Raya Rey A, Rebstock GA, Simeone A, Smith J, Van Buren A, Yorio P, García-Borboroglu P (2013) Magellanic penguins (*Spheniscus magellanicus*). In: García-Borboroglu P, Boersma PD (eds) *Penguins: natural history and conservation*. University of Washington Press, Seattle, pp 232–263
- Bonadonna F, Benhamou S, Jouventin P (2003) Orientation in “featureless” environments: the extreme case of pelagic birds. In: Berthold P, Gwinner E, Sonnenschein E (eds) *Avian migration*. Springer, Berlin Heidelberg, pp 367–377
- Bost C-A, Handrich Y, Butler P, Fahlman A, Halsey L, Woakes A, Ropert-Coudert Y (2007) Changes in dive profiles as an indicator of feeding success in king and Adélie penguins. *Deep Sea Res Part II* 54:248–255
- Bovet P, Benhamou S (1991) Optimal sinuosity in central place foraging movements. *Anim Behav* 42:57–62
- Capurro A, Frere E, Gandini M, Gandini P, Holik T, Lichtschein V, Boersma PD (1988) Nest density and population size of Magellanic penguins (*Spheniscus magellanicus*) at Cabo Dos Bahias, Argentina. *Auk* 105:585–588
- Carroll G, Everett JD, Harcourt R, Slip D, Jonsen I (2016) High sea surface temperatures driven by a strengthening current reduce foraging success by penguins. *Sci Rep* 6:1–13
- Castillo J, Yorio P, Gatto A (2019) Shared dietary niche between sexes in Magellanic penguins. *Austral Ecol*
- Ciancio JE, Yorio P, Wilson R, Frere E (2018) Food provisioning in Magellanic penguins as inferred from stable isotope ratios. *Rapid Commun Mass Spectrom* 32:489–494
- Ciancio JE, Yorio P, Buratti C, Colombo GÁ, Frere E (2021) Isotopic niche plasticity in a marine top predator as indicator of a large marine ecosystem food web status. *Ecol Indic* 126:107687
- Cotté C, Park Y, Guinet C, Bost C (2007) Movements of foraging king penguins through marine mesoscale eddies. *Proc R Soc B* 274:2385–2391
- Crawley M (2007) *The R book*. Wiley, Chichester
- Cresswell JE, Osborne JL, Goulson D (2000) An economic model of the limits to foraging range in central place foragers with numerical solutions for bumblebees. *Ecol Entomol* 25:249–255
- Croxall JP, Trathan PN, Murphy EJ (2002) Environmental change and Antarctic seabird populations. *Science* 297:1510–1514. <https://doi.org/10.1126/science.1071987>
- Cullen J, Chambers L, Coutin P, Dann P (2009) Predicting onset and success of breeding in little penguins *Eudyptula minor* from ocean temperatures. *Mar Ecol Prog Ser* 378:269–278
- Dehnhard N, Eens M, Demongin L, Quillfeldt P, Poisbleau M (2015) Individual consistency and phenotypic plasticity in rockhopper penguins: female but not male body mass links environmental conditions to reproductive investment. *PLoS ONE* 10:e0128776
- Del Caño M, Quintana F, Yoda K, Dell’Omo G, Blanco GS, Gómez-Laich A (2021) Fine-scale body and head movements allow to determine prey capture events in the Magellanic penguin (*Spheniscus magellanicus*). *Mar Biol* 168:1–15
- Dornhaus A, Collins EJ, Dechaume-Moncharmont F-X, Houston AI, Franks NR, McNamara JM (2006) Paying for information: partial loads in central place foragers. *Behav Ecol Sociobiol* 61:151–161
- Ehrlich MD, Martos P, Madirolas A, Sánchez RP (2000) Causes of spawning pattern variability of anchovy and hake on the Patagonian shelf ICES Council Meeting, pp 1–13
- Elliott KH, Woo K, Gaston AJ, Benvenuti S, Dall’Antonia L, Davoren GK (2008) Seabird foraging behaviour indicates prey type. *Mar Ecol Progress Ser* 354:289–303
- Fernandez SJ, Yorio P, Ciancio JE (2019) Diet composition of expanding breeding populations of the Magellanic penguin. *Mar Biol Res* 15:1–13
- Frere E, Gandini P, Lichtschein V (1996) Variación latitudinal en la dieta del pingüino de magallanes (*Spheniscus magellanicus*) en la costa Patagónica, Argentina. *Ornitología Neotropical* 7
- Furness R, Birkhead T (1984) Seabird colony distributions suggest competition for food supplies during the breeding season. *Nature* 311:655–656
- García Borboroglu P, Pozzi L, Yorio P (2019) Breeding range expansion and population distribution shifts of Magellanic Penguins in northern Patagonia, Argentina. In: Otago Uo (ed) *International Penguin Congress*, Dunedin
- Giudici PI, Quintana F, Svagelj WS (2017) The role of hatching asynchrony in a seabird species exhibiting obligate brood reduction. *Waterbirds* 40:221–232
- Glemboki NG, Williams GN, Góngora ME, Gagliardini DA, Orensanz JML (2015) Synoptic oceanography of San Jorge Gulf (Argentina): a template for Patagonian red shrimp (*Pleoticus muelleri*) spatial dynamics. *J Sea Res* 95:22–35

- Gómez-Laich A, Wilson RP, Sala JE, Luzenti A, Quintana F (2015) Moving northward: comparison of the foraging effort of Magellanic penguins from three colonies of northern Patagonia. *Mar Biol* 162:1451–1461. <https://doi.org/10.1007/s00227-015-2681-1>
- Guinet C, Koudil M, Bost CA, Durbec JP, Georges JY, Mouchot MC, Jouventin P (1997) Foraging behaviour of satellite-tracked king penguins in relation to sea-surface temperatures obtained by satellite telemetry at Crozet Archipelago, a study during three austral summers. *Mar Ecol Prog Ser* 150:11–20
- Hansen J, Martos P, Madirolas A (2001) Relationship between spatial distribution of the Patagonian stock of Argentine anchovy, *Engraulis anchoita*, and sea temperatures during late spring to early summer. *Fish Oceanogr* 10:193–206
- Karnauskas K, Jenouvrier S, Brown C, Murtugudde R (2015) Strong sea surface cooling in the eastern equatorial Pacific and implications for Galápagos Penguin conservation. *Geophys Res Lett* 42:6432–6437
- Krebs JR, Stephens DW, Sutherland WJ (1983) Perspectives in optimal foraging. Perspectives in ornithology. Cambridge University Press, Cambridge, pp 165–221
- Labraga JC (1994) Extreme winds in the Pampa del Castillo Plateau, Patagonia, Argentina, with reference to wind farm settlement. *J Appl Meteorol* 33:85–95
- Le Bohec C, Durant JM, Gauthier-Clerc M, Stenseth NC, Park Y-H, Pradel R, Gremillet D, Gendner J-P, Le Maho Y (2008) King penguin population threatened by Southern Ocean warming. *Proc Natl Acad Sci* 105:2493–2497
- Lescroël A, Bost C-A (2005) Foraging under contrasting oceanographic conditions: the gentoo penguin at Kerguelen Archipelago. *Mar Ecol Prog Ser* 302:245–261
- Pájaro M, Macchi GJ, Martos P (2005) Reproductive pattern of the Patagonian stock of Argentine hake (*Merluccius hubbsi*). *Fish Res* 72:97–108
- Palma ED, Matano RP, Piola AR (2004) A numerical study of the Southwestern Atlantic Shelf circulation: Barotropic response to tidal and wind forcing. *J Geophys Res Oceans* 109
- Parker GA, Smith JM (1990) Optimality theory in evolutionary biology. *Nature* 348:27–33
- Peters G, Wilson RP, Scolaro JA, Laurenti S, Upton J, Galleli H (1998) The diving behavior of Magellanic penguins at Punta Norte, Península Valdés, Argentina. *Colon Waterbirds* 21:1–10
- Pichegru L, Cook T, Handley J, Voogt N, Watermeyer J, Nupen L, McQuaid C (2013) Sex-specific foraging behaviour and a field sexing technique for Endangered African penguins. *Endanger Species Res* 19:255–264
- Pinheiro JC, Bates DM (2000) Linear mixed-effects models: basic concepts and examples. *Mixed-effects models in S and S-Plus*, pp 3–56
- Pisoni JP, Rivas AL, Piola AR (2015) On the variability of tidal fronts on a macrotidal continental shelf, Northern Patagonia, Argentina. *Deep Sea Res Part II* 119:61–68
- Ponchon A, Gremillet D, Christensen-Dalsgaard S, Erikstad KE, Barrett RT, Reiertsen TK, McCoy KD, Tveraa T, Boulinier T (2014) When things go wrong: intra-season dynamics of breeding failure in a seabird. *Ecosphere* 5:art4. <https://doi.org/10.1890/es13-00233.1>
- Pozzi LM, Borboroglu PG, Boersma PD, Pascual MA (2015) Population regulation in Magellanic penguins: what determines changes in colony size? *PLoS ONE* 10:e0119002. <https://doi.org/10.1371/journal.pone.0119002>
- Quintana F, Wilson R, Prandoni N, Svagelj W, Gómez-Laich A (2021) Long-term ecology studies in Patagonian seabirds: a review with the Imperial Cormorant as a case study. In: Helbling EW, Narvarte MA, González RA, Villafañe VE (eds) *Global change in Atlantic coastal Patagonian ecosystems: a journey through time*. Springer (in press)
- R Development Core Team (2019) A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing. Available from: <https://www.r-project.org>
- Raya Rey A, Bost C-A, Schiavini A, Pütz K (2010) Foraging movements of Magellanic penguins *Spheniscus magellanicus* in the Beagle Channel, Argentina, related to tide and tidal currents. *J Ornithol* 151:933–943
- Raya Rey A, Pütz K, Scioscia G, Lüthi B, Schiavini A (2012) Sexual differences in the foraging behaviour of Magellanic penguins related to stage of breeding. *Emu-Austral Ornithol* 112:90–96
- Raya Rey A, Rosciano N, Liljesthrom M, Samaniego RS, Schiavini A (2014) Species-specific population trends detected for penguins, gulls and cormorants over 20 years in sub-Antarctic Fuegian Archipelago. *Polar Biol* 37:1343–1360
- Romero SI, Piola AR, Charo M, Garcia CAE (2006) Chlorophyll-a variability off Patagonia based on SeaWiFS data. *J Geophys Res Oceans* 111:C05021. <https://doi.org/10.1029/2005jc003244>
- Ropert-Coudert Y, Chiaradia A, Ainley D, Barbosa A, Boersma PD, Brasso R, Dewar M, Ellenberg U, García-Borboroglu P, Emmerson L, Hickcox R, Jenouvrier S, Kato A, McIntosh RR, Lewis P, Ramirez F, Ruoppolo V, Ryan PG, Seddon PJ, Sherley RB, Vanstreels RET, Waller LJ, Woehler EJ, Trathan PN (2019) Happy feet in a hostile world? The future of penguins depends on proactive management of current and expected threats. *Front Mar Sci*. <https://doi.org/10.3389/fmars.2019.00248>
- Rosciano NG, Pütz K, Polito MJ, Raya Rey A (2018) Foraging behaviour of Magellanic penguins during the early chick-rearing period at Isla de los Estados, Argentina. *Ibis* 160:327–341
- Roy C, Van der Lingen C, Coetzee J, Lutjeharms J (2007) Abrupt environmental shift associated with changes in the distribution of Cape anchovy *Engraulis encrasicolus* spawners in the southern Benguela. *Afr J Mar Sci* 29:309–319
- Sala JE, Wilson RP, Frere E, Quintana F (2012a) Foraging effort in Magellanic penguins in coastal Patagonia, Argentina. *Mar Ecol Prog Ser* 464:273–287. <https://doi.org/10.3354/meps09887>
- Sala JE, Wilson RP, Quintana F (2012b) How much is too much? Assessment of prey consumption by Magellanic penguins in Patagonian Colonies. *PLoS ONE* 7:e51487. <https://doi.org/10.1371/journal.pone.0051487>
- Sala JE, Wilson RP, Frere E, Quintana F (2014) Flexible foraging for finding fish: variable diving patterns in Magellanic penguins *Spheniscus magellanicus* from different colonies. *J Ornithol* 155:801–817
- Sala JE, Pisoni JP, Quintana F (2017) Three-dimensional temperature fields of the North Patagonian Sea recorded by Magellanic penguins as biological sampling platforms. *Estuar Coast Shelf Sci* 189:203–215
- Schiavini A, Yorio P, Gandini P, Raya Rey A, Dee Boersma P (2005) Los pingüinos de las costas argentinas: estado poblacional y conservación. *El Hornero* 20:5–23
- Scioscia G, Rey AR, Schiavini A (2016) Breeding biology of Magellanic penguins (*Spheniscus magellanicus*) at the Beagle Channel: interannual variation and its relationship with foraging behaviour. *J Ornithol* 157:773–785
- Silva C, Andrade I, Yáñez E, Hormazabal S, Barbieri MÁ, Aranís A, Böhm G (2016) Predicting habitat suitability and geographic distribution of anchovy (*Engraulis ringens*) due to climate change in the coastal areas off Chile. *Prog Oceanogr* 146:159–174
- Simeone A, Wilson RP (2003) In-depth studies of Magellanic penguin (*Spheniscus magellanicus*) foraging: can we estimate prey consumption by perturbations in the dive profile? *Mar Biol* 143:825–831
- Sutton G, Pichegru L, Botha JA, Kouzani AZ, Adams S, Bost CA, Arnould JP (2020) Multi-predator assemblages, dive type, bathymetry and sex influence foraging success and efficiency in African penguins. *PeerJ* 8:e9380

- Tremblay Y, Cherel Y (2000) Benthic and pelagic dives: a new foraging behaviour in rockhopper penguins. *Mar Ecol Prog Ser* 204:257–267
- Weimerskirch H, Bonadonna F, Bailleul F, Mabile G, Dell’Omo G, Lipp H-P (2002) GPS tracking of foraging albatrosses. *Science* 295:1259–1259
- Wilson RP, Puetz K, Peters G, Culik B, Scolaro JA, Charrassin JB, Ropert-Coudert Y (1997) Long-term attachment of transmitting and recording devices to penguins and other seabirds. *Wildl Soc Bull* 25:101–106
- Wilson RP, Ropert-Coudert Y, Kato A (2002) Rush and grab strategies in foraging marine endotherms: the case for haste in penguins. *Anim Behav* 63:85–95
- Wilson RP, Scolaro JA, Grémillet D, Kierspel MA, Laurenti S, Upton J, Gallelli H, Quintana F, Frere E, Müller G (2005a) How do Magellanic penguins cope with variability in their access to prey? *Ecol Monogr* 75:379–401
- Wilson RP, Scolaro JA, Grémillet D, Kierspel MAM, Laurenti S, Upton J, Gallelli H, Quintana F, Frere E, Muller G, Straten MT, Zimmer I (2005b) How do Magellanic penguins cope with variability in their access to prey? *Ecol Monogr* 75:379–401
- Wilson RP, Jackson S, Straten MT (2007) Rates of food consumption in free-living Magellanic penguins *Spheniscus magellanicus*. *Mar Ornithol* 35:109–111
- Wilson RP, McMahon CR, Quintana F, Frere E, Scolaro A, Hays GC, Bradshaw CJ (2011) N-dimensional animal energetic niches clarify behavioural options in a variable marine environment. *J Exp Biol* 214:646–656
- Wilson R, Sala J, Gómez-Laich A, Ciancio J, Quintana F (2015) Pushed to the limit: food abundance determines tag-induced harm in penguins. *Anim Welf* 24:37–44
- Worton BJ (1989) Kernel methods for estimating the utilization distribution in home-range studies. *Ecology* 70:164–168
- Yorio P, Frere E, Gandini P, Harris G (1998) Atlas de la distribución reproductiva de aves marinas en el litoral Patagónico Argentino. Fundación Patagonia Natural Puerto Madryn
- Yorio P, González-Zevallos D, Gatto A, Biagioni O, Castillo J (2017) Relevance of forage fish in the diet of Magellanic penguins breeding in northern Patagonia, Argentina. *Mar Biol Res* 13:603–617. <https://doi.org/10.1080/17451000.2016.1273529>
- Zar JH (1999) Biostatistical analysis. Pearson Education India
- Zuur A, Ieno EN, Walker N, Saveliev AA, Smith GM (2009) Mixed effects models and extensions in ecology with R. Springer Science & Business Media

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