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**Article**

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# KEY MARINE AREAS DURING PENGUIN MIGRATION IN THE ARGENTINE SEA: CONTRIBUTIONS TO THEIR CONSERVATION KNOWLEDGE

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**ABSTRACT:** During migration, seabirds concentrate in key oceanic areas associated with high productivity. Magellanic Penguins (*Spheniscus magellanicus*) and Western Rockhopper Penguins (*Eudyptes chrysocome chrysocome*) spend most of the non-breeding season migrating in the Argentine Sea. Here, we compared the distances and phenology of migratory trips between both species breeding in nearby colonies (< 20 km apart in Puerto Deseado, Santa Cruz). In addition, we evaluated the association of these colonies and other Magellanic Penguin colonies with marine fronts during migration. Between 2017 and 2024, we analyzed 186 geolocators recovered from adult individuals of both species. Western Rockhopper Penguins traveled greater total distances and moved farther offshore than Magellanic Penguins, but the maximum distances reached were similar. Magellanic Penguins departed from and returned to the colony earlier than Western Rockhopper Penguins, exhibiting interspecific reproductive allochrony. The most frequently used front by both species was the El Rincón Front. In the case of Magellanic Penguins, the Río de la Plata Front appears to act as the eastern limit of migration for individuals from northern colonies (60% of the population evaluated), whereas the Patagonian Current Front is used by individuals from southern colonies (16%). Under thermal anomalies, Western Rockhopper Penguins also used the shelf-break front. These findings reveal spatial and temporal segregation in habitat use by these species and highlight the importance of key areas for their conservation, such as the waters of El Rincón and the Río de la Plata.

**KEYWORDS:** *Argentine Sea, marine fronts, migration, non-breeding season, penguins*

Penguins are mesopredators or apex predators and given their abundance and distribution, play key roles in the trophic webs of the Argentine Sea (Falabella et al. 2009, García-Borboroglu & Boersma 2013). Their breeding sites are generally easily accessible and this consequently allows assessments of their reproductive success, health, and year-round distribution at sea that can be used as environmental indicators of ocean conditions (Boersma 2008). Two penguin species primarily use the Argentine continental shelf: the Magellanic Penguin (MP, *Spheniscus magellanicus*) and the Western Rockhopper Penguin (WRP, *Eudyptes chrysocome chrysocome*; but see Baylis et al. 2015, Baylis et al. 2021). Both species spend much of their annual cycle at sea and are migratory species, but breed in terrestrial colonies. The MP forms colonies from Islote Lobos (40°47'S), at the northernmost point of its range, southward along the entire Argentine Patagonian mainland coast and the islands of Tierra del Fuego and the Malvinas Islands (Raya Rey et al.

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2014, Millones et al. 2021, García-Borboroglu et al. 2022). MP also breeds along the Chilean coast, from the southern tip northward to Isla Algarrobo (33°22'S, 71°40'W). The total population (Atlantic and Pacific) is estimated at 1.2–1.6 million pairs (Boersma et al. 2013) and is classified by the IUCN (International Union for Conservation of Nature) as 'Least Concern' (BirdLife International 2020a). The WRP breeds in several colonies in the Malvinas Islands, on Isla de los Estados, and on several other islands in southern Chile south of 51°S (Pütz et al. 2013). During the 1980s, a small colony was discovered on Isla Pingüino (47°54'S, 65°42'O), the northernmost point of its distribution (Frere et al. 1993). This species has a global population of 900,000 pairs (Pütz et al. 2013, Raya Rey et al. 2014, Gandini et al. 2017), and its conservation status is considered Vulnerable (BirdLife International 2020b). The WRP shares breeding areas with the MP, although they do not form mixed colonies (Boersma et al. 2013, Pütz et al. 2013).

Much research has focused on the trophic ecology and at-sea movements of these two penguin species during the breeding season, a period during which they are central-place foragers (Schiavini & Raya Rey 2004, Oehler et al. 2018, Ainley & Wilson 2023). However, the non-breeding period has been studied far less extensively (Stokes et al. 1998, Pütz et al. 2000, Pütz et al. 2007, Raya Rey et al. 2007). The non-breeding period is important because it is during this stage that individuals face the greatest risks from predation, disease, exhaustion, food shortages, and adverse weather conditions (Newton 2008), which can subsequently affect populations. More recently, the advent of new technologies that are less invasive for penguins, such as satellite devices (Clarke & Kerry 1994, Wilson et al. 2004, Wilson et al. 2015), together with decreasing costs, has led to new studies providing information from different colonies and covering complete penguin migrations (Yamamoto et al. 2019, Barrionuevo et al. 2020, Dodino et al. 2021, Barrionuevo et al. 2023, Green et al. 2023).

Southern Atlantic MPs migrate northward from their colonies (Stokes et al. 1998, Pütz et al. 2007, Yamamoto et al. 2019, Barrionuevo et al. 2020, Dodino et al. 2021, Barrionuevo et al. 2023, Rebstock & Boersma 2023). However, partial migration occurs in this species: in colonies located in the southern portion of its range, some individuals migrate whereas others remain near their breeding colonies (Barrionuevo & Frere 2024). The areas used during this dispersal depend on the colony studied, with individuals also segregating in the environmental and trophic niches they occupy (Barrionuevo et al. 2023), resulting in extensive use of the Argentine shelf during winter. In addition, there is sex-based segregation, with females migrating closer to the coast than males (Yamamoto et al. 2019, Barrionuevo et al. 2020, Rebstock & Boersma 2023). In contrast, WRP migration differs substantially depending on the breeding colony (Pütz et al. 2002, Pütz et al. 2006a, Raya Rey et al. 2007, Ratcliffe et al. 2014, Green et al. 2023, Barrionuevo et al. 2025). Penguins from the Isla de los Estados colony migrate southward and then westward toward the Pacific Ocean, occasionally entering the Southern Ocean (Green et al. 2023). In contrast, penguins from the Isla Pingüino colony migrate northward while remaining on the Argentine shelf (Barrionuevo et al. 2025). In the Malvinas Islands, individuals follow one or the other migratory pattern depending on the colony (Ratcliffe et al. 2014). No sex-based segregation in space use during migration (Thiebot et al. 2015) or during the pre-molt trip (Dodino et al. 2024) has been found in this species. Recently, the migration of individuals of both species breeding in Puerto Deseado, Santa Cruz, one of the sites where they coexist, was analyzed using geolocators and stable isotopes (Barrionuevo et al. 2025). The results showed that WRPs differ from MP in both isotopic and spatial niche use, with the former concentrating their migration more along the shelf break and in the El Rincón region, whereas MPs migrate off Peninsula Valdés and San Matías Gulf, using to a lesser extent the waters off Buenos Aires Province and the Río de la Plata. Nevertheless, both species occupy relatively similar environmental niches, although MP use shallower and warmer waters than WRP (8.6°C vs. 11°C, Barrionuevo et al. 2025).

During migration, penguins may use marine fronts as key areas. Key marine areas are regions of the ocean with exceptionally high biological productivity where the structure of marine fronts (contact zones between different water masses) generates predictable aggregations of prey (Alemany et al. 2009). In the Argentine Sea, these fronts act as biological 'magnets' that facilitate foraging by penguins, as well as other seabirds and marine megafauna, by concentrating nutrients and biomass at specific locations along the shelf break and continental shelf (Falabella et al. 2009, Piola et al. 2018). Indeed, marine fronts are selected by many species because of their environmental characteristics and the presence of high concentrations of key prey (e.g., small fish and pelagic crustaceans). The spatial coincidence between fronts and primary production is generally very high (e.g., Acha et al. 2004), but it gradually decreases as higher trophic-level organisms are considered because, due to their larger size, greater locomotory capacity, and more complex behavior, they are more independent of their environment (Alemany et al. 2018). In addition, from a physical perspective, a front can be defined as a line connecting points of maximum horizontal gradient in a given variable (typically temperature or salinity). Although this definition is conceptually correct, it has limited relevance for ecological studies because organisms do not live along a line; rather, they occur and concentrate within a region of 'frontal influence'. Therefore, fronts may be highly important for species even when there is little overlap with the line that physically defines the front (Acha et al. 2024).

It is during the aquatic phase, such as migration, that penguins face the greatest anthropogenic risks. Although both MPs and WRPs are exposed on land to anthropogenic threats associated with global change—such as exposure to high temperatures or extreme rainfall during the breeding season, resulting in increased chick and even adult mortality (Boersma & Rebstock 2014, Holt & Boersma 2022, Lera et al. 2023)—when at sea, bycatch in fisheries is moderately important, particularly for MPs, with records of mortality in gillnet and trawl fisheries (Crawford et al. 2017). Although mortality rates reported in specific studies are relatively low and do not compare with those of other pelagic seabird species (Favero et al. 2011, Tamini et al. 2015), they could still be important considering the cumulative effects across the species' extensive distribution, where it overlaps with different types of fisheries (Crawford et al. 2017). Another anthropogenic threat to which penguins on the Argentine shelf are exposed is oil exploitation. This was a major cause of MP mortality during the 1980s and 1990s, with an estimated 40,000 penguins dying annually during that period (Gandini et al. 1994). However, oil-related mortality rates have now declined dramatically due to appropriate mitigation measures (see Wagner et al. 2023). During episodes of seismic surveying in the oceans, associated with the exploration and exploitation of new hydrocarbon resources, highly intense artificial sounds are produced, which have been shown to temporarily reduce the abundance of Magellanic Penguins in affected areas (Seco Pon et al. 2019). On the other hand, contamination through the ingestion of marine debris is very common in juvenile penguins stranded along the coast (Di Beneditto et al. 2017, Seco Pon et al. 2023). However, except in rare cases, it is not a direct cause of mortality (Neto et al. 2021). This issue has been infrequently reported in breeding adults. Microplastics have also been found in feces of penguins admitted to rehabilitation centers (Mendez-Sanhueza et al. 2023), and various tissues have been found contaminated with organochlorines and heavy metals (Baldassin et al. 2016, Quadri-Adrogué et al. 2022); however, the actual impact of these contaminants on individuals remains unknown. Currently, global changes in the oceans are considered a potentially major threat to these species (Trathan et al. 2015), but evaluating this hypothesis requires a deeper understanding of the issue. To date, evidence has only been found in Western Rockhopper Penguins, including alterations in migratory patterns associated with sea-surface temperature anomalies (Raya Rey et al. 2007, Barrionuevo et al. 2025) and records of high mortality during the pre-molt trip stage that could not be attributed to other causes such as disease outbreaks (Boersma 1987, Morgenthaler et al. 2018). Projections of oceanic changes, particularly those related to sea-surface temperature and sea-surface height, indicate a reduction in preferred habitat for WRPs using the Pacific Ocean, but an expansion of habitat for those using the Atlantic Ocean (Green et al. 2023). Therefore, studies on the species' plasticity and its ability to adapt to new environmental scenarios will be highly important for conservation efforts.

To improve our understanding of migration and identify key marine areas used by both species, we established the following specific objectives: 1) To compare the characteristics of migratory trips (e.g., distances traveled and reached, phenology, and travel direction) of individuals of both species breeding in Puerto Deseado, Santa Cruz. 2) To evaluate the use of marine fronts by these species during migration. Subsequently, in the Discussion, based on the results obtained, we address the potential risks posed by different anthropogenic activities during migratory trips in both species.

## METHODS

### Study Sites

For the migratory study of the WRP, we worked with individuals from Isla Pingüino (47°54'S, 65°42'W), located in Santa Cruz, Argentina. This island lies within the interjurisdictional park Marino Isla Pingüino and hosts a recently established Western Rockhopper Penguin colony totaling 1581 breeding pairs. This colony has been increasing at a rate of 7.7% since 1985 (Gandini et al. 2017) and is probably the result of immigration from colonies in the Malvinas Islands (Gandini et al. 2017, Lois et al. 2020). Magellanic Penguins also breed on this island

(10,169 breeding pairs; Millones et al. 2021).

For the migratory study of MPs, we used three colonies distributed across almost the entire latitudinal extent of the species' breeding range. Much of the information compiled on migration from these colonies can be found in Barrionuevo et al. (2023). The colonies were: a) Estancia San Lorenzo (42°05'S, 63°54'W), located in the northern part of the breeding range, with a population of 240,000 breeding pairs, making it the largest colony of the species. This colony increased its population by 92% since the 1990s (Garcia-Borboroglu et al. 2022). b) Isla Quiroga, located within the Deseado Estuary and forming part of the Ría Deseado Provincial Reserve, situated 20 km from Isla Pingüino. It hosts 1,348 pairs of Magellanic Penguins and is surrounded within a 10-km radius of nearly 25,000 pairs, constituting a stable population (Millones et al. 2021). c) Finally, Cabo Vírgenes, located at the southern end of the breeding range, is the third-largest colony with 127,000 breeding pairs and has shown a 42% increase over the last 30 years (Millones et al. 2021).

### Fieldwork

During the late breeding season or molting period (February to March), between 2017 and 2024, we deployed 186 geolocators: 159 MK4 and 27 MK3 units (geolocator weight: 1.80 g and 2.5 g, respectively; less than 0.1% of the animals' body mass; Lotek, UK) on adult MPs and WRPs to track them during migration. The different models vary in their precision, with the MK4 representing a newer generation. These devices are attached to the tarsus using cable ties covered with heat-shrink tubing to avoid harming the animals (Ratcliffe et al. 2014b) and can be deployed relatively quickly, requiring less than three minutes. The devices were recovered when penguins returned from migration (September/October for MPs and November for WRPs). In the Supplementary Material, Table 1 shows the number of devices analyzed for each year and colony. Recovery averaged approximately 78.03% across all study years. In this study, we used only data from the migratory trip, excluding the pre-molt trip (see Statistical Analyses for details on how this distinction was made).

Penguins were captured at their nests by the leg using a specially reinforced hook designed to avoid injury. Males have a slightly wider bill than females, which allows sex determination (Gandini et al. 1992).

### Statistical Analyses

To download geolocator data, we used the Bastrack software (BioTrack 2013), and analyses were conducted using the R package *TwGeos* (Lisovski et al. 2015) in R (R Development Core Team 2021). Geolocators do not record positions directly; instead, they record natural light intensity every minute, storing the highest value every 5 min. They also record the state of the device (wet/dry) and temperature after a continuous period of 25 min in the same state. Therefore, to estimate positions, we defined twilight events (sunrises/sunsets) using the threshold method. Specifically, we selected an arbitrary threshold of 1.5 light units for all individuals and, for each trip, selected calibration periods to estimate a sun elevation angle and the error distribution (Lisovski et al. 2020). We then calculated 1000 possible migratory trajectories by modifying twilight times according to the twilight error distribution, resulting in 1000 location estimates per twilight event that represented the expected spatial distribution of possible locations. Finally, we used the R package *SGAT* (Wotherspoon et al. 2016) and Bayesian Markov Chain Monte Carlo (MCMC) methods to refine movement trajectories by incorporating prior information on the expected twilight error distribution, a spatial mask delimiting land and sea areas, a sea-surface temperature mask for calibration with temperature records from the device, and a movement model. Additional details can be found in Lisovski et al. (2020) and Barrionuevo et al. (2023).

For the first objective, comparing migratory-trip characteristics between MPs and WRPs breeding at nearby sites, we used only data from Isla Quiroga and Isla Pingüino. These colonies are located close to one another (~20 km apart), making comparisons between species more appropriate. In addition, we used only years for which sufficient data were available for both species (2019, 2021, 2022, and 2024).

To define departure from and arrival at the colony, we used the wet/dry state of the device because penguins rarely leave the water once migration begins. Departure was defined as the day on which records remained continuously wet for more than six hours, allowing short dry-state events (30 min), whereas arrival was defined as the day on which records remained continuously dry for more than six hours, allowing short dry-state events (30 min). This information was used to estimate migratory-trip duration. When data from the pre-molt trip were available (during which penguins also remain in the water for extended periods), this data was excluded.

To calculate trip characteristics, we used the R package *track2KBA* (Beal et al. 2021), considering only the most probable trip for each individual. For each individual, we calculated the maximum distance reached (from the colony to the farthest point in a straight line), total distance traveled, and angular direction (the angle between the farthest point and the colony location, using geographic north as 0°).

These variables were then used, one at a time, as response variables in linear models (package *nlme*, Pinheiro et al. 2023). Predictor variables included sex, species, study year, the two-way interactions between species and sex and between species and year, and the three-way interaction. A total of 64 models were generated using the dredge function in the *MuMin* package (Bartón 2023). Models were ranked according to the Akaike Information Criterion corrected for small sample sizes (AICc). Following a parsimony criterion, we considered all models with ΔAICc < 4 to be competitive. To obtain robust parameter estimates, we performed model averaging across this set of models. To evaluate whether a predictor was informative within this model set, we examined its 95% confidence intervals using the *confint* function. Predictor variables whose confidence intervals included zero were considered non-informative, whereas those excluding zero were considered important in explaining variation in the response variable (Grueber et al. 2011). For informative variables, post hoc multiple comparisons were performed using Estimated Marginal Means (EMMeans) with the *emmeans* package (Lenth 2024), using a significance level of $\alpha = 0.05$.

For the second objective, evaluating overlap between penguin-use areas and marine fronts, we determined the location of fronts present during the cold season based on the climatological distribution of sea-surface temperature (SST) and salinity gradients, as reported by Acha et al. (2020). To estimate the degree of overlap, we used the complete migratory-trip dataset. First, we created a spatial occurrence-density map from the trips of each penguin colony. Map cells had a resolution of 0.25° × 0.25°. We then converted density values to a scale ranging from 0 to 1 and retained cells with the highest occurrence values (1–0.3), removing low-occurrence cells. Finally, we overlaid these cells with the cells corresponding to each marine front, retaining the number of cells overlapping the front. This value was then divided by the total number of high-occurrence penguin cells to obtain a percentage overlap.

## RESULTS

### Migratory Trips of Magellanic Penguins (MPs) and Western Rockhopper Penguins (WRPs)

Maximum distance reached was best explained by the null model. However, both species and sex were included in the three additional models that were also considered plausible, but these variables were deemed non-informative because their 95% confidence intervals (CI) included zero (Supplementary Material Table 2; mean ± SD: WRP = 1208 ± 206 km, $n$ = 42; MP = 1166 ± 490 km, $n$ = 65).

Total distance traveled was greater in WRPs than in MPs (mean ± SD: WRP = 8651 ± 2360 km, $n$ = 39; MP = 6778 ± 2325 km, $n$ = 64; Fig. 1; Supplementary Material Table 2): according to the multimodel analysis, species was the only informative predictor (95% CI excluded zero; Supplementary Material Table 3), being the main factor in the best-supported models. Sex and the interaction between species and sex were present in the important models; however, they were considered non-informative. Post hoc analyses confirmed that differences between species were consistent for both sexes (WRP–MP contrast: Females: Estimate ± SE = 1901 ± 511, t-ratio = 3.72, $p < 0.00$; Males: Estimate ± SE = 1834 ± 511, t-ratio = 3.59, $p < 0.00$).

Angular direction was explained by a set of four models with AIC < 4 (Supplementary Material Table 2). One model included study year, species, and the interaction between both factors as predictors. Another model also included sex, and a final model additionally included the interaction between sex and species (Supplementary Material Table 2). However, only year and its interaction with species were informative predictors (95% CI excluded zero). The direction of all MP trips was, on average ± SD, 36.7 ± 24.5° NE (range = 32°–44.3°, $n$ = 65), whereas that of WRPs was 47 ± 32.6° NE (range = 36.3°–73.7°, $n$ = 42). Notably, in 2021, WRPs traveled at an angle of 73.7 ± 17.2° NE, moving farther east than usual (Fig. 2). This difference was statistically significant between WRPs in 2021 and MPs in 2022 and 2024 (Post hoc contrasts: WRP:2021–MP:2022 Estimate ± SE = 40.46 ± 10.76, t-ratio = 3.76, $p = 0.01$; WRP:2021–MP:2024 Estimate ± SE = 39.08 ± 11.36, t-ratio = 3.44, $p = 0.02$; Supplementary Material Table 3). The remaining contrasts were not significant ($0.11 < p < 1$; WRP:2021–WRP:2022 $p = 0.07$). In addition, neither sex nor its interactions contributed significant information to the model (Supplementary Material Table 3).

The model with the lowest AIC explaining migration departure date included sex, study year, species, and the interaction between species and year. However, four additional models were also important and included the interaction between species and sex (Fig. 1; Supplementary Material Table 2). Informative predictors were the year × species interaction, as well as year and species (all excluded zero in their 95% CI). MPs left the colony earlier than WRPs in all years (mean ± SD: WRP = 110 ± 8.17 days (~ April 20), $n$ = 45; MP = 99 ± 4.91 days (~ April 9), $n$ = 67), regardless of sex, with no significant differences between males and females within each species (sex contrasts: WRP $p = 0.61$, MP $p = 0.57$; Supplementary Material Table 3). Departure date showed a significant interaction between year and species ($p = 0.01$; Supplementary Material Table 2). This effect was due to an exceptional delay in WRPs during 2021, when individuals departed for their wintering areas on average on day 116 ± 2 (~ April 26), significantly later than in 2019 (mean ± SE: 106 ± 2; Post hoc $p = 0.01$) and 2024 (106 ± 2; Post hoc $p = 0.02$). In contrast, MPs showed remarkable interannual stability in departure dates (mean range: 98–100; all interannual contrasts $p > 0.90$). Because of this asymmetric shift, the temporal difference between both colonies doubled in 2021, reaching 16.1 days ($p < 0.00$) compared to the 7.90 days observed in 2019 ($p = 0.02$).

Arrival date at the colony (end of migration) was explained by two relevant models (AIC < 4) that included species, sex, study year, and the interaction between sex and species (Fig. 1; Supplementary Material Table 2). Species, year, and sex were informative predictors (95% CI excluded zero; Supplementary Material Table 3). MPs arrived at colonies earlier than WRPs (Post hoc Estimate ± SE = 22 ± 1.70, t-ratio = 12.96, $p > 0.00$; mean ± SE: WRP = 290 ± 5.94 days (~ October 17), $n$ = 36; MP = 268 ± 11 days (~ September 25), $n$ = 64). Regarding annual variation, post hoc contrasts confirmed a significant difference between 2019 and 2022 among penguins (Estimate ± SE = 7.07 ± 2.09 days, t-ratio = 3.38, $p = 0.06$). The remaining interannual contrasts were not significant after adjustment for multiple comparisons ($p > 0.16$). Males always arrived earlier than females, regardless of species and year (Post hoc, Estimate ± SE = 8.25 ± 1.66, t-ratio = 4.96, $p < 0.00$). Thus, MP males were the first to arrive, followed by MP females, which arrived before WRP males, while WRP females were the last to complete migration (mean ± SE: Julian day: MP♂ = 264 ± 7, MP♀ = 274 ± 13, WRP♂ = 287 ± 4, WRP♀ = 294

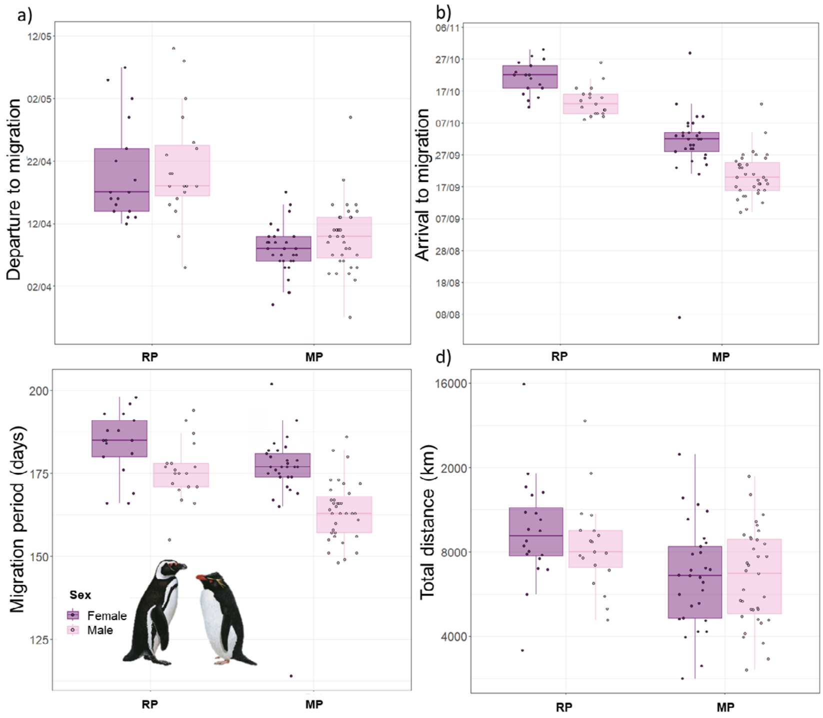

**Figure 1.** Characteristics of the migratory trips of Magellanic Penguins (*Spheniscus magellanicus*) from Isla Quiroga and Western Rockhopper Penguins (*Eudyptes chrysocome*) from Isla Pingüino, both breeding near Puerto Deseado, Argentina. Boxplots show sex differences in: (a) departure dates, (b) arrival dates (years pooled), (c) migration duration (total number of days), and (d) total distance traveled (km). Boxes represent the first and third quartiles (25% and 75%), lines within boxes indicate the median, whiskers indicate the interquartile range, and points represent individual values. Darker symbols correspond to females and lighter symbols to males.

± 5; Supplementary Material Table 3).

The duration of the migratory period was explained by two models that included year, species, sex, and the sex × species interaction (Fig. 1; Supplementary Material Table 2). Among these predictors, the interaction was the only non-informative variable (95% CI included zero). Male migration lasted fewer days than female migration (mean ± SD: ♂ = 168 ± 11 days, $n$ = 54; ♀ = 179 ± 13 days, $n$ = 46; Supplementary Material Table 2). WRPs spent more days at sea than MPs (mean ± SD: WRP = 180 ± 10 days, $n$ = 36; MP = 169 ± 13 days, $n$ = 64). In addition, post hoc contrasts showed that migration lasted longer in 2019 than in 2021 and 2022 (respectively; $p$ = 0.04, $p$ = 0.02; Supplementary Material Table 3).

### Relationship Between Migratory Trips and Marine Fronts

These species used different areas of the continental shelf (Figs. 2 & 3). In addition, MPs used different areas depending on the breeding colony, with a tendency for individuals from more northern colonies to use more northern regions. WRPs used the El Rincón region, although during 2021 they also occupied the shelf-break area (Fig. 2).

The most heavily used front by penguins was the El Rincón Front, which was extensively visited by the northern and central MP colonies, as well as by a smaller proportion of individuals from southern colonies and by WRPs (Fig. 3, Table 1). The shelf-break front was used primarily by WRPs. The Patagonian Current Front was used to a lesser extent by central MPs and extensively by MPs from the southern portion of the distribution (Fig. 3, Table 1). The Río de la Plata Front did not overlap with the distribution of penguins from any of the colonies studied.

In this study, we found interspecific differences in the migratory trip characteristics of Magellanic Penguins (MP) and Western Rockhopper Penguins (WRP) breeding in very close colonies in Puerto Deseado. We also found differences in the intensity of marine front use according to colony and species. Particularly important for these species was the El Rincón Front region, which includes waters at the mouth of San Matías Gulf in Río Negro and those of southern Buenos Aires Province, and which also constitutes a Marine National Park and Nature Reserve.

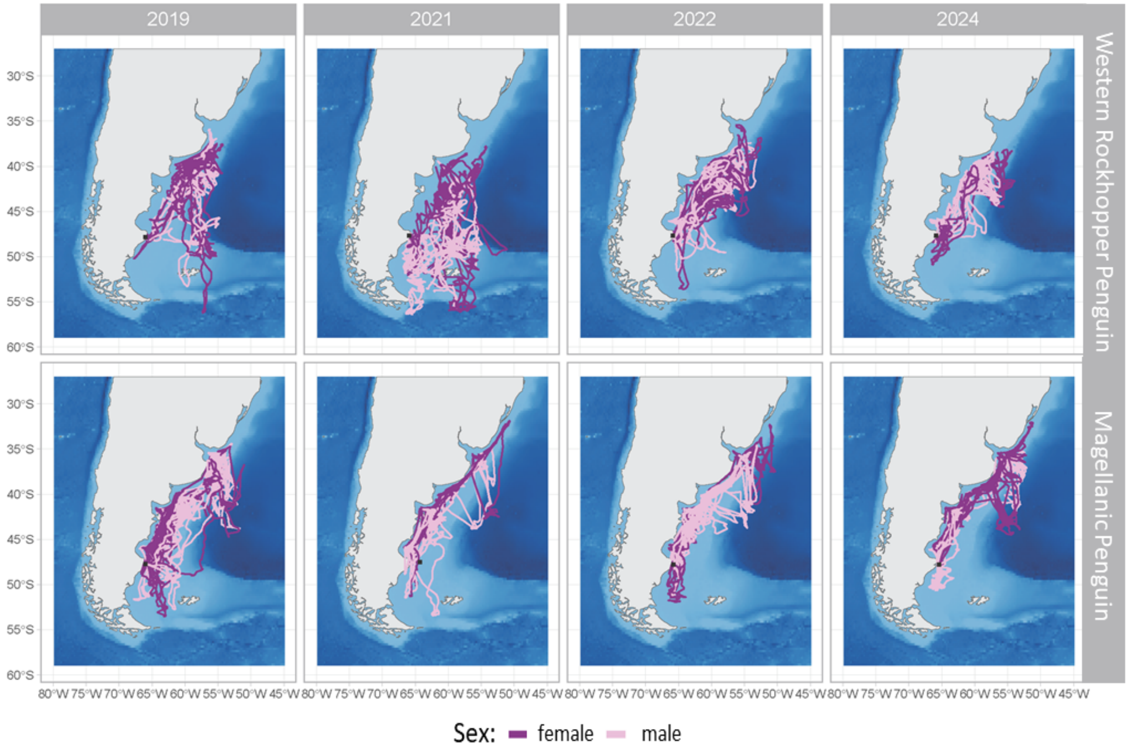

**Figura 2.** Migratory trips of Magellanic Penguins (*Spheniscus magellanicus*) from the Isla Quiroga colony and Western Rockhopper Penguins (*Eudyptes chrysocome*) from the Isla Pingüino colony, Santa Cruz, Argentina. Trips from the four years (2019, 2021, 2022, and 2024) for which data from both species were available are included. Colonies are indicated by black squares. Lighter tracks correspond to males and darker tracks to females. The x-axis shows longitude, and the y-axis shows latitude. Shades of blue indicate estimated sea depth.

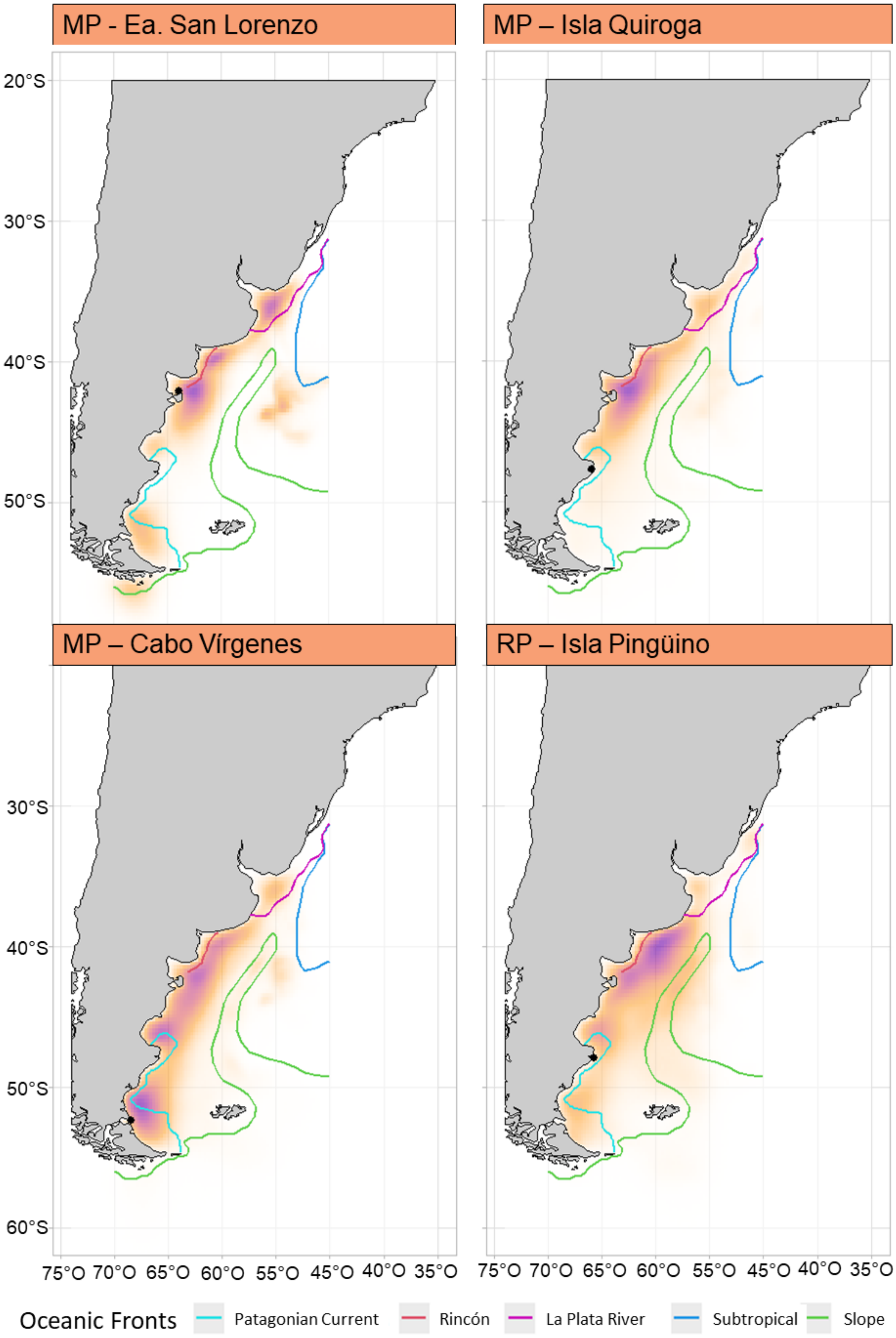

**Figura 3.** Occurrence density maps during migration for Magellanic Penguins (*Spheniscus magellanicus*; MP) from three colonies and Western Rockhopper Penguins (*Eudyptes chrysocome*; RP) breeding on Isla Pingüino. Occurrence was standardized from 0–1, where 1 represents the highest occurrence and 0 the lowest, and is displayed using a continuous color gradient from violet (1) to white (0). Colony locations are indicated by solid black circles. Colored lines represent different marine fronts, identified in the legend (modified from Acha et al. 2020).

Previous studies conducted at Isla Quiroga and Isla Pingüino have shown that MPs and WRPs partially share the areas used during migration, with greater overlap in their oceanographic niche (chlorophyll concentrations, temperature, salinity), but not in their isotopic niche—demonstrating differences in diet (Barrionuevo et al. 2025). To complete the understanding of migratory segregation, it was necessary to compare trip parameters. Regarding migratory trip characteristics, WRPs traveled nearly 2000 km more than MPs. This difference in distance is probably not due to a greater swimming capacity of WRPs, as they are even slightly smaller than MPs (Boersma et al. 2013, Pütz et al. 2013). In addition, WRPs dive to shallower average depths than MPs during the breeding season (Pütz et al. 2006b, Sala et al. 2014, Dehnhard et al. 2016, Rosciano et al. 2022). The difference cannot be explained by the maximum distance reached either, as we found no differences between species, nor by migration duration, because although WRP migration lasted 10 days longer than MP migration, this is insufficient to explain an additional 2000 km traveled. Therefore, the greater distance traveled is likely associated with greater daily movement by WRPs relative to MPs. In both species, females migrated longer than males, although this difference was much greater in MPs (15 more days versus 8 more days in WRPs). The difference in migration duration between sexes is explained by differences in arrival dates (MP males arrived 10 days earlier than females, and WRP males 7 days earlier than females), since departure dates were similar between sexes within species. In general, male penguins arrive earlier than females at nesting sites to prepare and defend their nests (Boersma et al. 2013). There were also differences between species in departure and arrival dates; MPs departed on migration approximately 11 days earlier than WRPs and also returned to the colony earlier than WRPs; the difference was 23 days between MP and WRP males and 17 days between females. This translates directly into a difference in the reproductive phenology of the species. At the study site, the average laying dates of first eggs are October 10 for MPs and November 7 for WRPs (Lera et al. 2023).

During migration, penguins would be expected to use marine fronts; however, given their diet, we would not expect complete overlap between marine fronts and penguin habitat use. MPs feed primarily on fish, such as *Engraulis anchoita* and *Sprattus fuegensis*, but also consume squid and crustaceans (Boersma et al. 2013, Ciancio et al. 2021). In contrast, WRPs feed at lower trophic levels, consuming larvae of those fish species, squid, and crustaceans (Pütz et al. 2013). In this regard, we found that different colonies used the fronts of the Argentine shelf differently. WRPs from Isla Pingüino used fronts to a lesser extent than MPs. Only 15% of the most heavily used WRP locations overlapped with the El Rincón Front and 8% with the shelf-break front. However, the El Rincón region was the area most used by this species. The shelf-break front region was particularly important in 2021, when positive sea surface temperature anomalies occurred (Barrionuevo et al. 2025), demonstrating its potential importance as a refuge under global warming scenarios.

For MPs, we could divide the Argentine breeding population into three groups (excluding the Malvinas Islands population) according to available information on colony location, population size, and migration patterns. 1) Northern colonies, represented in this study by Estancia San Lorenzo, would include those in Río Negro and Chubut (García-Borboroglu et al. 2022) and account for 62.4% of the total Argentine population. In this case, MP distribution overlapped extensively with the El Rincón Front. Although it did not overlap with another front, the Río de la Plata Front, which constitutes the eastern boundary of the river plume (Piola et al. 2008), appears to act as an eastern boundary for these individuals as well. This front separates estuarine waters from marine waters; penguins using the region west of this front are probably capturing prey of estuarine or coastal origin.

**Table 1.** Use of marine fronts on the Argentine continental shelf by Western Rockhopper Penguins (*Eudyptes chrysocome*) and Magellanic Penguins (*Spheniscus magellanicus*) (shown by colony). Values are expressed as the percentage that each front represents within the total number of highest-use cells for each colony.

| Especie | Front Colony | Patagonian Current | El Rincón | Slope | Subtropical | La Plata River |
|---|---|---|---|---|---|---|
| Western Rockhopper Penguins | Isla Pingüino | 0 | 15.38 | 7.59 | 0 | 0 |
| Magellanic Penguins | San Lorenzo | 0 | 92.31 | 0 | 0 | 0 |
| | Isla Quiroga | 1.61 | 69.23 | 0 | 0 | 0 |
| | Cabo Vírgenes | 40.32 | 15.38 | 0 | 0 | 0 |

2) Colonies in the central portion of the MP breeding distribution could include those from northern and central Santa Cruz, from Punta Pájaros to Monte León (Millones et al. 2021), and comprise 21.4% of the total population. Penguins from the center of the distribution are represented in this study by the Isla Quiroga colony and primarily used the El Rincón Front (70%) and, to a lesser extent, the Patagonian Current Front (1.6%). 3) Finally, southern colonies, including those from southern Santa Cruz (Millones et al. 2021) and Tierra del Fuego (Raya Rey et al. 2004), represent 16.2% of the population. This group is represented in our study by the Cabo Vírgenes colony, whose penguins used the Patagonian Current Front (40%) and the El Rincón Front (15%).

The northern (1) and central (2) sectors of the MP breeding distribution, which comprise most of the population, as well as the WRP colony studied, preferentially used the El Rincón area. This front extends approximately from 39°S to 41°S, is located in shallow coastal waters, and is present year-round (Acha et al. 2004). It is situated off the south-southeastern coast of Buenos Aires Province and includes the mouth of San Matías Gulf. This area represents one of the country's most important hydrocarbon development zones, including the Bahía Blanca petrochemical complex, and soon it will be developed as an oil and gas loading area, with the installation of offshore buoys and degassing vessels in San Matías Gulf. On the other hand, it is an area of relatively low fishing effort, with seasonal fishing closures during much of the year (Copello et al. 2014). Both the industrial bottom-trawl fleet and the artisanal longline fleet operate here. The former operates year-round, although with lower effort during the winter months when penguins use these waters. Nevertheless, direct or indirect interactions may occur in the area through incidental penguin bycatch or even through the capture of non-target species such as the Argentine Anchovy (see Gandini et al. 1998). Although there are records of incidental penguin bycatch in Argentine Hake (*Merluccius hubbsi*) and Patagonian Red Shrimp (*Pleoticus muelleri*) trawl fisheries, its incidence does not appear to be very high (Gandini et al. 1998, González-Zeballos & Yorio 2006, Crawford et al. 2017).

The northern colonies of the MP distribution, which represent 62% of the population analyzed in this study, used the Río de la Plata estuary region. The Río de la Plata plume forms a low-salinity, nutrient-rich area whose extent depends primarily on river discharge and wind intensity and direction (Piola et al. 2008). It has been reported that variation in plume extent strongly influenced the reproductive success of MPs at Punta Tombo (Rebstock & Boersma 2018), a colony belonging to the northern sector according to our categorization of the species' national distribution. In terms of commercial fishing, this area is important for both offshore and coastal fresh-fish fleets. It is a fishing ground for some penguin prey species, although overall fishing effort and total catches are not high (Copello et al. 2014). There are few records of direct interactions between penguins and these fleets (e.g., Tamini et al. 2002, Seco Pon et al. 2013).

The shelf-break front, which was used primarily by WRPs during anomalous years, is a permanent front extending along the continental shelf break from Burdwood Bank eastward, around the Malvinas Islands, and northward to the confluence of the Malvinas and Brazil Currents (Acha et al. 2004). There are two major fisheries in this region, targeting Argentine Hake and Argentine Shortfin Squid (*Illex argentinus*), but available data indicate that neither has a significant direct effect on penguins in the area (Tamini et al. 2015, Crawford et al. 2017). In contrast, the Patagonian Current Front was heavily used by the southern sector of the MP distribution, although this sector represents only 16% of the population studied. This front is critical for the breeding and distribution of adult penguin prey species such as the Fuegian Sprat (*Sprattus fuegensis*; Madirolas et al. 2000) and *Grimothea gregaria* (Diez et al. 2016).

In summary, fronts associated with the waters of Buenos Aires Province appear to be key feeding areas for penguins, particularly MPs, during the non-breeding period. WRPs also use these fronts, although to a much lesser extent. Fortunately, commercial fisheries do not currently appear to represent a major problem during the winter months for penguins using this region, either through competition for prey or bycatch (Crawford et al. 2017). Identifying the areas most heavily used during penguin migration and ensuring their protection, particularly from large-scale extractive activities, is essential for the conservation of penguins breeding in the Argentine Sea. This is especially important in the context of expanding hydrocarbon development on the continental shelf and ongoing global change, for which there is already evidence of impacts on marine areas of the Argentine continental shelf (Franco et al. 2020).

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## SUPPLEMENTARY MATERIAL

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