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Department of Arctic and Marine Biology

**Spatial segregation by sympatrically breeding Antarctic and Snow Petrels.**

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Master's thesis in Biology BIO-3950 - May 2024

# Master's thesis

# Spatial segregation by sympatrically breeding Antarctic and Snow Petrels.

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Cover image: Antarctic and Snow petrels drawing by Yuna Philippot

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# ABSTRACT

Sympatrically breeding species may face intense competition for resources, which can lead to various forms of segregation to mitigate competitive pressures. Segregation of space or habitats is one possible strategy, particularly when species share similar diets and foraging behaviors. This study examines the differences in space and habitat use between Antarctic and Snow Petrels (*Thalassoica antarctica* and *Pagodroma nivea)* breeding at the Svarthamaren colony (Dronning Maud Land, Antarctica), by using fine-scale tracking data. We analyzed the characteristics of their foraging trips, estimated the foraging areas, and assessed the overlap between them. Additionally, we quantified their sea-ice use at foraging locations and compared them between the two species, with the prediction that Snow petrels were more associated to sea-ice than Antarctic Petrels. The results indicate that Antarctic Petrels traveled on average at faster speeds, covered greater distances, and for longer durations during incubation than Snow Petrels. During chick-rearing, however, Snow Petrels traveled further than Antarctic Petrels, the difference in speed remained the same. These two petrel species showed clear spatial segregation, during both incubation and chick-rearing, with their foraging areas overlapping by less than 20%. Antarctic Petrels generally traveled northeast of the colony while Snow Petrels traveled westwards and closer to the shore. As predicted, Snow Petrels were 45% less likely to use areas without sea-ice compared to Antarctic Petrels when foraging. This study provides valuable insights into the at-sea space use and habitat preferences of these relatively understudied species during the breeding season. It underscores the importance of segregation strategies for their coexistence and emphasizes their dependence on sea-ice, particularly for Snow Petrel, rendering them potentially vulnerable to the loss of sea-ice due to climate change.

# 1. INTRODUCTION

Understanding how species share space and resources is a central problem in ecology. Interspecific interactions play a crucial role in determining spatial distribution and habitat utilization among species. A species' use of the environment can be described by its ecological niche, which was defined by Hutchinson (1957) as the multi-dimensional space that is uses, including abiotic and biotic factors. However, species may alter their habitat use to decrease interspecific competition. Species are predicted to segregate by adjusting at least one dimension of their niche to avoid direct competition (Schoener 1974). This adjustment results in what is called the realized niche, as opposed to the fundamental niche, which corresponds to the environment an animal would use in the absence of competition (Hutchinson 1957). This phenomenon allows the co-existence of the two species in the same environmental space (Gause 1934, Hutchinson 1957, Schoener 1974, Volterra 1928).

As ecological niches have a multitude of dimensions, there are numerous ways in which animals can achieve niche segregation: for example, through diet (Connan *et al.* 2014, Steenweg *et al.* 2011), but also through their use of space or habitat (Delord *et al.* 2016, Kappes *et al.* 2015, Petalas *et al.* 2024, Picket *et al.* 2018). A thorough analysis of interspecific segregation requires examining all dimensions of species' niches, which is rarely achievable. A more manageable approach would focus on at least one dimension of the niche. Although this does not provide a full description of the Hutchinsonian niche, it still offers valuable information to better understand interspecific relationships and species coexistence (Hutchinson 1957, Petalas *et al.* 2024).

The significance of spatial segregation becomes especially apparent in the context of sympatrically breeding seabirds. Seabirds are central-place foragers during the breeding season, which means they return to the colony between each foraging trip. When breeding sympatrically, they must share limited foraging space especially when they have similar foraging behavior and feed on the same resources. Competition can increase in such systems, leading to potential niche segregation (Connan *et al.* 2014, Granroth-Wilding & Phillips 2019, Phillips *et al.* 2005, Pickett *et al.* 2018) either by specializing on different resources (Connan *et al.* 2014, Croxall & Prince 1980, Steenweg *et al.* 2011) or by using different foraging areas and thus by spatially segregating (Granroth-Wilding & Phillips 2019, Phillips *et al.* 2005, Pickett *et al.* 2018).

Foraging strategies change during the breeding season to accommodate the changing energetic requirements of the parents and their offspring (Ito *et al.* 2010, Phillips *et al.* 2017). During incubation, the foraging parent has the opportunity to embark on long trips, as their adult partner on the nest can survive a long period of time without eating (Hedd *et al.* 2004). When chicks hatch, however, they need to be fed regularly (Ito *et al.* 2010, Péron *et al.* 2010, Phillips *et al.* 2017, Rickleffs 1983). The foraging behavior is then optimized by the foraging parent, usually by traveling shorter distances and by increasing the feeding frequency (Ito *et al.* 2010, Phillips *et al.* 2017). Such differences in the constraints associated to incubation and chick feeding may affect the potential competition between species, and lead to different patterns of spatial segregation.

In this master thesis we aimed to assess the difference in the space and habitat use of the Antarctic Petrel *Thalassoica antarctica* and Snow Petrel *Pagodroma nivea* breeding at the Svarthamaren colony in Dronning Maud Land, Antarctica, and to test for spatial segregation between the two species. To our knowledge, no study of the spatial segregation between these two species has been done before. These two closely related Fulmarine Petrels are Antarctic endemic species (Marchant & Higgins 1990). They are found all around Antarctica and share a very similar life-history and foraging ecology. They both breed from late November to early March, during the Austral summer, and feed on the same resources, including krill, fish and squid (Ferretti *et al.* 2001, Griffiths 1983, Lorentsen *et al.* 1998, Marchant & Higgins 1990). Both Antarctic and Snow Petrels are associated with sea-ice habitats (Ainley *et al.* 1984, Fauchald *et al.* 2017, Griffiths 1983, Tarroux *et al.* 2020) although this association might be less pronounced in Antarctic Petrels (Tarroux et al. 2020).

Using fine-scale tracking data from GPS loggers in summer 2022/2023, we first described the foraging trip characteristics of Antarctic and Snow Petrel. Since the Antarctic Petrel is larger but has a similar wing load as the Snow Petrel (Griffiths 1983, Marchant & Higgins 1990), we predicted that the Antarctic Petrel would undertake longer trips and fly faster. We also predicted that the birds would undertake shorter trips during chick-rearing compared to incubation, due to the demands of chick provisioning, which necessitates shorter foraging trips for both species. (Marchant & Higgins 1990).

Second, we quantified the spatial overlap in Antarctic and Snow Petrel foraging areas, with the prediction that the species would spatially segregate to avoid competition leading to a limited overlap of their foraging areas.

Third, we assessed their sea-ice use at foraging locations. We predicted the Snow Petrel's foraging behavior to be more closely associated with sea-ice than the Antarctic Petrel. Indeed, previous studies have suggested that Antarctic Petrels were typically more associated with open water near the sea-ice edge, whereas Snow Petrels were more likely to utilize areas with greater sea-ice concentration (Ainley *et al.* 1984, Hoyo *et al.* 1992, Steele 2005).

# 2. METHODS

## 2.1. Study species and data collection.

Antarctic Petrels and Snow Petrels belong to the order Procellariformes and the family Procellariidae. They feed on fish, cephalopods, and crustaceans (Ferretti *et al.* 2001, Griffiths 1983, Lorentsen *et al.* 1998, Marchant & Higgins 1990) and are central place foragers during the breeding season. Both species have a similar breeding phenology, laying their egg in late-November to early December for Antarctic Petrels and early to mid-December for Snow Petrels, with hatching occurring early/ mid-January and mid/late January for Antarctic and Snow Petrels, respectively (Hoyo *et al.* 1992, Marchant & Higgins 1990).

The Antarctic Petrel weighs approximately 675 g with a body length of 40 to 45 cm and a wingspan of 100 to 110 cm. It is distributed all around Antarctica. It breeds in snow-free areas and nests on shallow depressions in rocks with gravel; it lays only one egg that is incubated for approximately 45 days before hatching. The chick-rearing period also lasts approximately 45 days (Marchant & Higgins 1990).

The Snow Petrel weighs approximately 300 g, with a body length between 30 to 40 cm, and a wingspan ranging from 75 to 95 cm. It is distributed throughout Antarctica and has a strong association with pack-ice areas when feeding at sea (Ainley *et al.* 1984). They breed in cavities in exposed rocks, laying one egg per year, with an incubation period of approximately 45 days and chick-rearing period of 48 days (Marchant & Higgins 1990).

The Svarthamaren colony is located 200 km away from the coast at 71°53'S, 5°10'E (Mehlum *et al.* 1988, Fig 1). Svarthamaren is one of the largest inland seabird colonies in Antarctica (Mehlum *et al.* 1988). In recent years, there have usually been between 20 000 and 120 000

breeding pairs of Antarctic petrels at Svarthamaren (Descamps *et al.* 2016, 2023), and approximately 2 000 breeding pairs of Snow Petrels *(Descamps, unpublished data).* The colony is more easily accessible than most due to its proximity to the Norwegian Troll airfield and research station (Mehlum *et al.* 1988). This colony has been studied intermittently for 40 years, enhancing our understanding of the foraging habitat use of Antarctic Petrels (e.g. Fauchald *et al.* 2017, Tarroux *et al.* 2020).
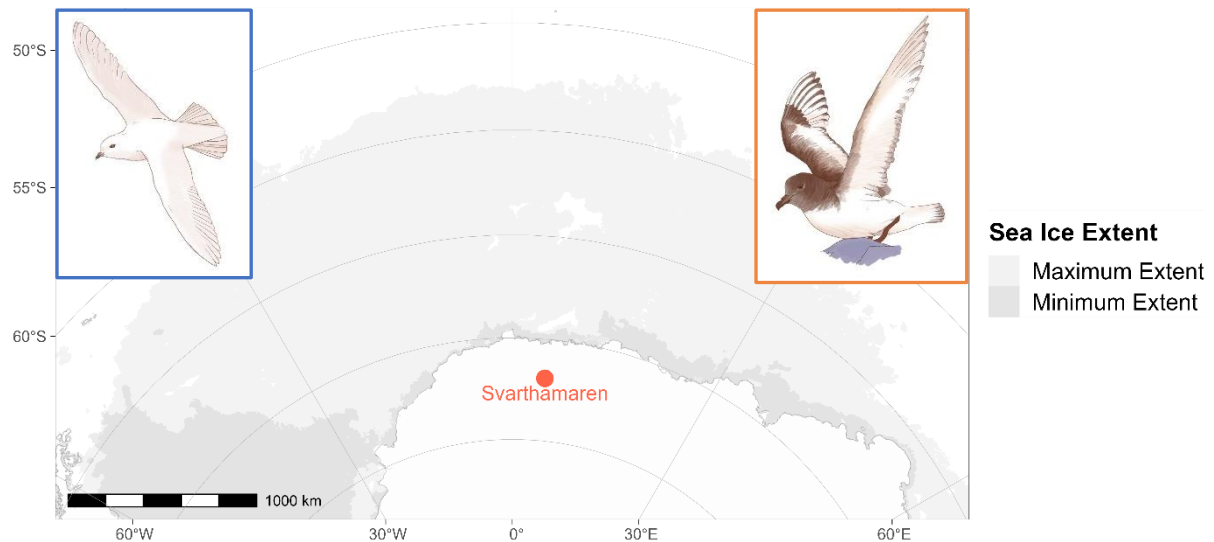


**Figure 1:** Location of the Svarthamaren colony in Dronning Maud Land, Antarctica. Illustrations include the Antarctic Petrel on the top right (orange) and the Snow Petrel on the top left (blue), along with the maximal and minimal sea-ice extent observed between December 2022 and February 2023.

GPS loggers were deployed on Antarctic Petrels (Pathtrack nanoFix GEO+RF) and Snow Petrels (Pathtrack nanoFix GEO+RF with solar panel) breeding at Svarthamaren, during the austral summer season of 2022-2023. Table 1a shows the number of birds on which loggers were deployed, as well as the reasons for any bird's exclusion from the study. The GPS loggers were deployed by taping them to the two central tail feathers and recorded locations every 30 min. The loggers weighed approximately 4 g for Snow Petrels and 4.5 g for Antarctic Petrels, which is less than 1.5% of the birds' body mass. Most of the time, loggers were deployed on birds that were about to be replaced by their partner on the nest and to start their foraging trip. Data from the loggers were downloaded from a distance with fixed solar base stations placed near the birds' nests. Table 1b shows the number of birds available for analysis and their breeding status.

**Table 1:** (1a) Number of Antarctic and Snow Petrel on which GPS loggers have been deployed, the reasons and number of birds not included in the analysis and the time period of the deployment. (1b) Number of GPS loggers deployed during the 2022-2023 breeding season on Antarctic and Snow Petrels. Incubation, chick-rearing and unknown indicates the nest status of the birds at trip's departure.

**(1a)**

| Species | | Snow Petrel | Antarctic Petrel |
|---|---|---|---|
| Deployed | | 45 | 38 |
| Non usable | Lost GPS | 5 | 12 |
| | No explanation | 4 | 0 |
| | No locations | 0 | 1 |
| | After processing: | 6 | 3 |
| Total available for analysis | | 30 | 22 |
| Time period | | 02/12/22 - 12/01/23 | 06/12/22 - 17/01/23 |

**(1b)**

| | Antarctic Petrel | Snow Petrel |
|---|---|---|
| Total for analyses | 22 | 30 |
| Incubation | 13 | 19 |
| Chick-rearing | 9 | 11 |
| Unknown | 0 | 5 |

## 2.2.  Data preparation

All data processing and analyses were performed using R software version 4.3.1 (R Core Team 2023).

The data was separated into individual trips with the tripSplit() function from the "Track2KBA" package (Beal *et al.* 2021). To do so, we defined a buffer of 35 km around the colony and all birds going outside this buffer were considered as starting a foraging trip. To determine if the trips were completed, we used a buffer of 1 km around the colony, and birds returning within this buffer were considered to have completed their trip. These parameters were determined through data exploration and represent a trade-off between the number of trips to include and their relevance to our question, specifically whether the birds reached the sea. Then, based on a previous study in the same system (Tarroux *et al.* 2016), we defined trips as foraging if they lasted at least 3 h. Trips were discarded if they had no return date,

gaps between consecutive locations greater than 12 hours, or if there was a distance greater than 200 km missing between the colony and the first or last point of the trip.

We operated per trip the Correlated Random Walk (CRW) model from the aniMotum package (Jonsen *et al.* 2023) to fill the gaps in our tracks, with a 30-minute interval between each coordinate. This model assumes that movements are random but follow a predictable pattern in both bearing and speed. Our starting parameters, used to determine the improbable locations, were a maximum travel speed of 40 m/s, an angle between 5 and 10 degrees and a distance between 5 000 and 10 000 m. This model infers animal movements, fills gaps, and reduces the impact of biases caused by equipment malfunctions, thereby providing a more reliable dataset for further analysis.

Table 2 displays the number of trips obtained, their breeding status, and the number of locations (before and after applying the CRW model) for both species.

**Table 2:** Number of trips and locations obtained after data preparation. The nest status (i.e. incubation, chick-rearing, unknown) corresponds to the status at the departure of the trip. "CRW" is the Correlated Random Walk model used to fill gaps.

|  | Antarctic Petrel | Snow Petrel |
|---|---|---|
| Number of trips | 51 | 60 |
| ➔ During incubation | 20 | 27 |
| ➔ During Chick-rearing | 31 | 28 |
| ➔ Unknown | 0 | 5 |
| Number of locations | 10 682 | 9 171 |
| ➔ After "CRW" | 14 014 | 15 282 |

Due to the low number of trips with "Unknown" nest status, and because they occurred only for the Snow Petrel, they were not considered in the analyses that required separation by nest status.

## 2.3. Foraging trip characteristics

To describe petrel foraging trips, we calculated five variables: (i) the cumulative distance traveled, (ii) the maximum distance from the colony, (iii) the duration, (iv) the mean speed, and (v) the bearing.

To obtain the cumulative distance, maximal distance, duration, and bearing of the trips, the function tripSummary() from the package track2KBA (Beal *et al.* 2021) was used. Distances are great circle distances, and the bearing corresponds to the angle between the colony and the furthest point of the trip. Angles greater than 180 degrees were transformed into their negative counterparts by subtracting 360 degrees.

To assess the mean speed of each foraging trip, we first calculated the distance (in kilometers) traveled between each coordinate using the distGeo() function from the geosphere package (Karney 2013). The speed was then calculated by dividing this distance by the time interval of half an hour.

To test for a difference in foraging trip characteristics between species and breeding status, we used generalized linear mixed models with the lme() function from the nlme package (Pinheiro *et al.* 2002). The bird identity and trip identity were included in all models as nested random factors, to take into account the hierarchical structure of the data (Schielzeth *et al.* 2013). We considered different models including species and/or breeding status as fixed effects as well as their interaction.

We used an Akaike Information Criterion (AIC) based model selection approach (Burnham and Anderson 2002), with five different models considered (Table SM1). If the difference in AIC values between two models was <2, the models had similar statistical support and in the case of nested models, the simplest one (i.e., with fewer parameters) was preferred (Burnham and Anderson 2002). For this model selection, a maximum likelihood (ML) was used to fit the models, as all models considered here had the same random effect structure but different fixed effects. However, to obtain unbiased estimates of the different effects, the selected models were rerun using restricted maximum likelihood (REML; Vasdekis *et al.* 2005, Zuur *et al.* 2009).

Total distance, maximum distance, and trip duration were highly correlated (Pearson's r > 0.85; Table SM2). Therefore, only the maximum distance traveled was considered in the analyses, as results from the other two metrics would be similar.

## 2.4. Spatial segregation in foraging areas

We filtered out positions on land using a medium-resolution shapefile from Quantarctica defining Antarctica's border (Matsuoka *et al.* 2018). This choice was made because the two

species do not forage on land; by eliminating these coordinates greater precision was achieved in our behavioral model.

The petrels' foraging areas were identified using Hidden Markov Models (HMM), with the momentuHMM package (McClintock *et al.* 2018). This method allows the attribution of a behavioral state at each position, based on the step length and angle between consecutive locations. This method has been used previously with Antarctic Petrels at the same site (Tarroux *et al.* 2020). The models were based on Weibull and Wrapped Cauchy distributions and considered the same five states as in Tarroux et al (2020; see Table 3). To run these HMM models, the same starting parameters as in Tarroux et al (2020) were used.

To ensure the model's effectiveness, we compared the proportion and locations of the behavioral states to existing knowledge about how these birds forage at sea. It is suspected that the models may have overestimated foraging states. This could be partly due to the exclusion of land coordinates, which decreased the proportion of transiting states. Additionally, the half-hour interval between location recordings could mask more frequent transitions between states, as foraging generally requires more time than transiting. However, such overestimation of the foraging state did not affect our main conclusions about spatial segregation between the two species (see Results and Discussion).

**Table 3:** Description of the behavioral states used in the HMM models. Step length is the distance between two successive bird's locations, and angle is the angle defined by three consecutive locations.

|   | Interpreted behavioral state | Step length | Angle |
|---|---|---|---|
| 1 | Rest/ drifting | Very short | Small range |
| 2 | Fine scale foraging | Short | Large range |
| 3 | Coarse scale foraging | Intermediate | Intermediate range |
| 4 | Transiting | Long | Small range |
| 5 | Fast transiting | Very long | Small range |

To identify the main foraging areas, only locations associated with foraging (i.e. states 2 and 3) were considered. We calculated the 95% utilization distribution (UD) using a kernel density estimate with the kernelUD() function from the adehabitatHR package (Calenge 2006). A UD describes the probability that an animal is found at a particular location (Worton

1989). We chose the 95% UD cumulative volume contour to describe birds' foraging areas. The grid was set to a size of 3 125 m, which matches the resolution of the sea-ice concentration data (see below). The 'href' ad-hoc smoothing method was applied. This method assumes that the animal's locations follow a bivariate normal distribution and that the smoothing parameters are the same in both x and y directions. Although it has the downside of potentially overestimating the UD, it was selected because other methods tested tended to highly underestimate the UD, leading to potentially under-estimated spatial segregation. The overlap between the 95% UD foraging areas of Antarctic and Snow Petrels was then calculated, using the kerneloverlap() function (Calenge 2006), and the Home Range (HR) method (Fieberg & Kochanny 2005). This method gives the proportion of each species UD that overlaps with the other species ranging from 0 (no overlap) to 1 (complete overlap). A HR analysis was chosen, as it gives results that are clear and straightforward to interpret. Other approaches, such as the Utilization Distribution Overlap Index (UDOI), gave similar results (Fig. SM2).

To quantify the uncertainty in the HR overlap, we used a bootstrap approach, with 500 iterations, using custom written code. At each iteration, the foraging locations from 22 Antarctic Petrels and 30 Snow Petrels (individuals resampled with replacement) were randomly selected and the overlap was calculated. The 95th percentile of these 500 overlap scores was then used to estimate the uncertainty around the HR overlap. The bootstrap was run first solely on the foraging locations and then also on all locations (including resting and traveling). This latter step, based on all coordinates, only aimed at confirming that the overlap between Snow and Antarctic Petrels was low (see results) whatever the approach used to identify potential foraging areas.

## 2.5. Use of sea-ice

To compare the use of sea-ice habitats by the two species, we extracted the sea-ice concentration at each petrel location. The sea-ice concentration dataset from Bremen University was used, which covers the 2022-2023 Austral summer season. These sea-ice concentration are obtained by applying the ARTIST Sea Ice algorithm to the brightness temperature obtained by the AMSR2 sensors from the JAXA satellite (Spreen *et al.* 2008). This dataset is organized into daily raster, where each cell is a 3 125 m square containing a

value that indicates the percentage of the cell covered by ice ranging from 0 (open water) to 100 (complete sea-ice cover).

Zero-inflated beta regression mixed models were used (with the bird identity and trip identity nested in bird identity, as random factors) as such models are suitable for handling concentration values, bounded between 0 and 1. Additionally, the zero-inflated component of the model allows to handle the large number of zeros present in the dataset. The glmmTMB() function from the glmmTMB package (Brooks *et al.* 2017) was used. We first considered the foraging locations only and then on all locations.

The same AIC-based model selection approach used for the foraging trip metrics was also employed for testing for a species difference in the sea-ice concentration, as detailed in the appendix (Table SM3).

# 3. RESULTS

## 3.1. Foraging trip characteristics

A detailed summary of these metrics is presented in Table 4, and the results of the mixed linear models in Table 5. The trips are mapped in the appendix (Fig. SM1).

The Antarctic Petrels trips range from 37 to 312 hours in duration, with maximal distances from 270 km to 1 810 km. There is a noticeable difference between the incubation (median = 277 hours and 1 546 km) and chick-rearing periods (median = 65 hours and 436 km). Conversely, Snow Petrels exhibit shorter trips, with durations ranging from 61 to 264 hours and maximal distances from 295 km to 1 513 km. The decrease from incubation (median = 159 hours and 637 km) to chick-rearing (median = 97 hours and 530 km) is less pronounced than for Antarctic Petrels. These differences between the two species are supported by our model selection, indicating that a *species×status* interaction best explained the variation in distance traveled (Tables 4 and 5, Fig. 2).

Regarding the direction of the trips, the bearing varied between species and breeding status (the model including *species×status* had the lowest AIC, see Tables 4 and 5). Antarctic Petrels generally head north (median = -1 degrees during incubation and -6 degrees during chick-rearing), while Snow Petrels generally head west (median = -64 degrees during incubation and -68 degrees during chick-rearing). Differences according to status are also observed, with Snow Petrels heading more to the east by a median difference of 4 degrees,

while Antarctic Petrels head more to the west, by a median difference of 5 degrees (Tables 4 and 5; Fig. 3).

As for speed, we observed a variation between species, with Antarctic Petrels travelling faster, but no variation between breeding status. Antarctic Petrels maintain a median speed of 22 km/h across both breeding stages, whereas Snow Petrels have a median speed of 18 km/h (Tables 4 and 5, Fig. 4).

**Table 4**: Summary of the foraging trip metrics for Antarctic and Snow Petrels during incubation and chick-rearing. The duration is in hours (h), the cumulative and maximal distance in km, the mean speed in km/h and the bearing in degrees.

| | Antarctic Petrel | | Snow Petrel | |
|---|---|---|---|---|
| | Incubating | Chick-rearing | Incubating | Chick-rearing |
| **Duration** | | | | |
| Mean (SD) | 266.8 (35.2) | 62.5 (15.0) | 152.7 (61.4) | 103.0 (29.5) |
| Median (IQR) | 276.8 (64.3) | 64.5 (24.0) | 159.0 (102.8) | 96.8 (36.9) |
| Range | 207.0 - 312.0 | 36.5 - 95.5 | 67.0 - 264.0 | 61.0 - 186.0 |
| **Cumulative Distance** | | | | |
| Mean (SD) | 5892.9 (967.5) | 1444.8 (432.8) | 2622.2 (1085.5) | 1935.7 (565.8) |
| Median (IQR) | 5700.6 (987.7) | 1336.9 (551.5) | 2322.0 (2060.1) | 1887.0 (563.0) |
| Range | 4255.5 - 8456.7 | 731.6 - 2232.0 | 1202.9 - 4594.6 | 1080.3 - 3431.3 |
| **Maximal Distance** | | | | |
| Mean (SD) | 1437.3 (276.2) | 462.1 (162.5) | 818.7 (381.1) | 603.0 (199.1) |
| Median (IQR) | 1546.0 (406.8) | 435.7 (180.4) | 636.5 (600.7) | 529.8 (209.7) |
| Range | 934.7 - 1810.4 | 269.9 - 852.8 | 405.5 - 1513.4 | 295.2 - 1109.2 |
| **Bearing** | | | | |
| Mean (SD) | 8.5 (38.8) | -4.7 (22.5) | -60.4 (21.2) | -66.6 (29.6) |
| Median (IQR) | -1.4 (62.4) | -5.9 (30.0) | -64.3 (25.0) | -68.2 (16.1) |
| Range | -74.9 - 74.2 | -39.6 - 42.3 | -96.3 - -3.2 | -117.3 - 48.7 |
| **Mean speed** | | | | |
| Mean (SD) | 22.0 (2.2) | 22.4 (4.7) | 18.3 (3.8) | 18.9 (4.4) |
| Median (IQR) | 21.6 (3.3) | 22.3 (7.3) | 17.7 (5.1) | 18.3 (4.8) |
| Range | 18.7 - 27.0 | 14.7 - 30.8 | 12.4 - 26.5 | 9.6 - 31.2 |

**Table 5:** Variation among breeding status and species in the foraging trip metrics. Results represent the output of the best model selected for each metric based on AIC (see Table SM1)

| Predictors | Total distance | | | Maximal distance | | | Duration | | | Bearing | | | Mean Speed | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Estimates | CI | p | Estimates | CI | p | Estimates | CI | p | Estimates | CI | p | Estimates | CI | p |
| (Intercept) | 1455 | 1024 – 1887 | <0.001 | 467 | 332 – 601 | <0.001 | 63 | 41 – 85 | <0.001 | -5 | -21 – 11 | 0.530 | 22 | 21 – 24 | <0.001 |
| Species [Snow Petrel] | 500 | -89 – 1088 | 0.094 | 145 | -41 – 331 | 0.123 | 44 | 14 – 74 | 0.005 | -57 | -78 – -35 | <0.001 | -4 | -6 – -2 | <0.001 |
| Status [Incubating] | 4502 | 3905 – 5098 | <0.001 | 983 | 794 – 1172 | <0.001 | 206 | 175 – 236 | <0.001 | 13 | -9 – 34 | 0.253 | | | |
| Species [Snow Petrel] Ã— Status [Incubating] | -3752 | -4527 – -2977 | <0.001 | -753 | -1003 – -504 | <0.001 | -155 | -195 – -116 | <0.001 | -10 | -38 – 18 | 0.496 | | | |
| **Random Effects** | | | | | | | | | | | | | | | |
| σ² | 57025.34 | | | 6449.15 | | | 138.78 | | | 69.51 | | | 1.41 | | |
| τ00 | 519.54 tripID | | | 150.20 tripID | | | 27.40 tripID | | | 20.00 tripID | | | 2.12 tripID | | |
| | 589.56 BIRDID | | | 211.23 BIRDID | | | 28.27 BIRDID | | | 19.79 BIRDID | | | 3.18 BIRDID | | |
| N | 106 tripID | | | 106 tripID | | | 106 tripID | | | 106 tripID | | | 106 tripID | | |
| | 49 BIRDID | | | 49 BIRDID | | | 49 BIRDID | | | 49 BIRDID | | | 49 BIRDID | | |
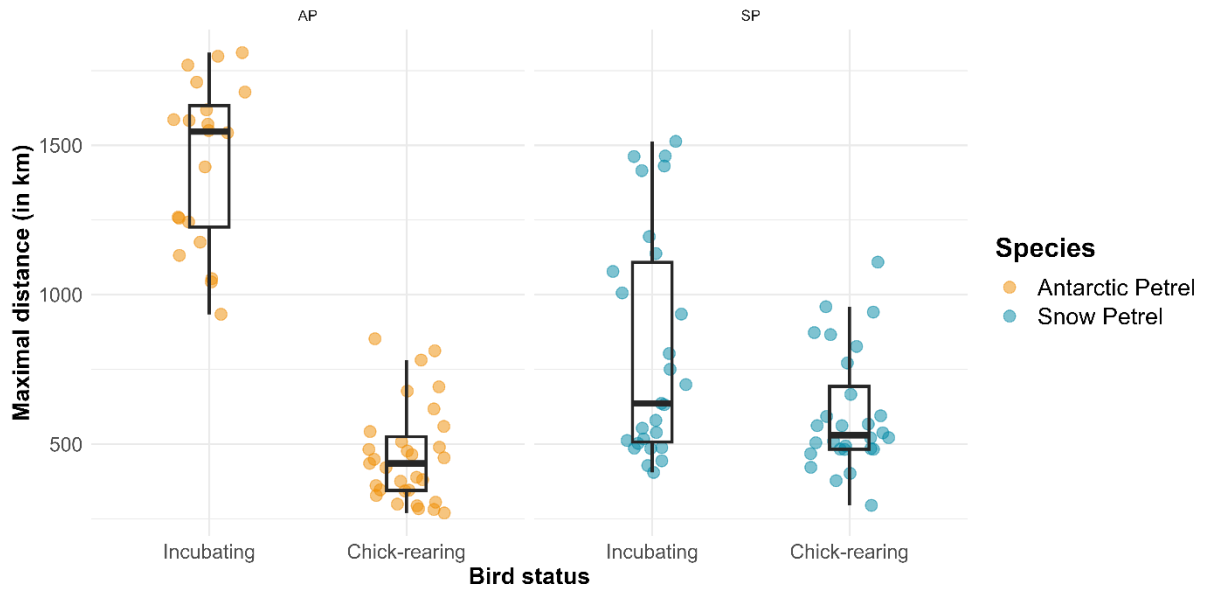
**Figure 2:** Boxplots of the maximal distance reached by individuals during foraging trips per nest status and species. The colored points represent the values attributed to each trip, with jittering along the x-axis to increase visibility. The horizontal line is the median, the box represents the interquartile range (IQR), and the whiskers are the upper and lower quartile ± 1.95×IQR.
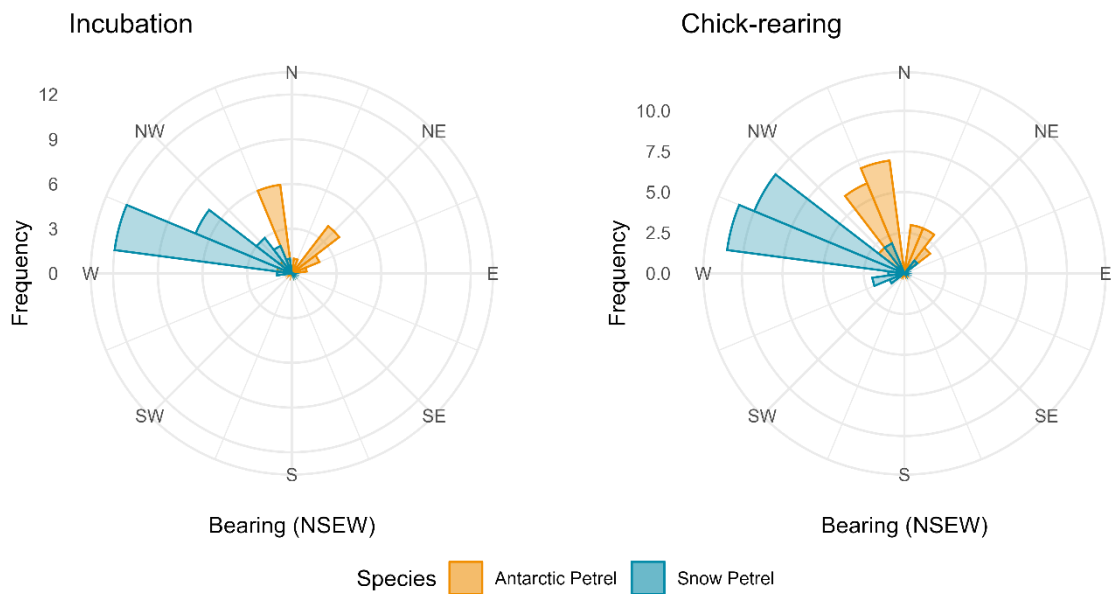


**Figure 3:** Bearing taken by Antarctic and Snow Petrels depending on their nest status. The bearing represents the angle between the colony and the furthest point reached during the foraging trip.
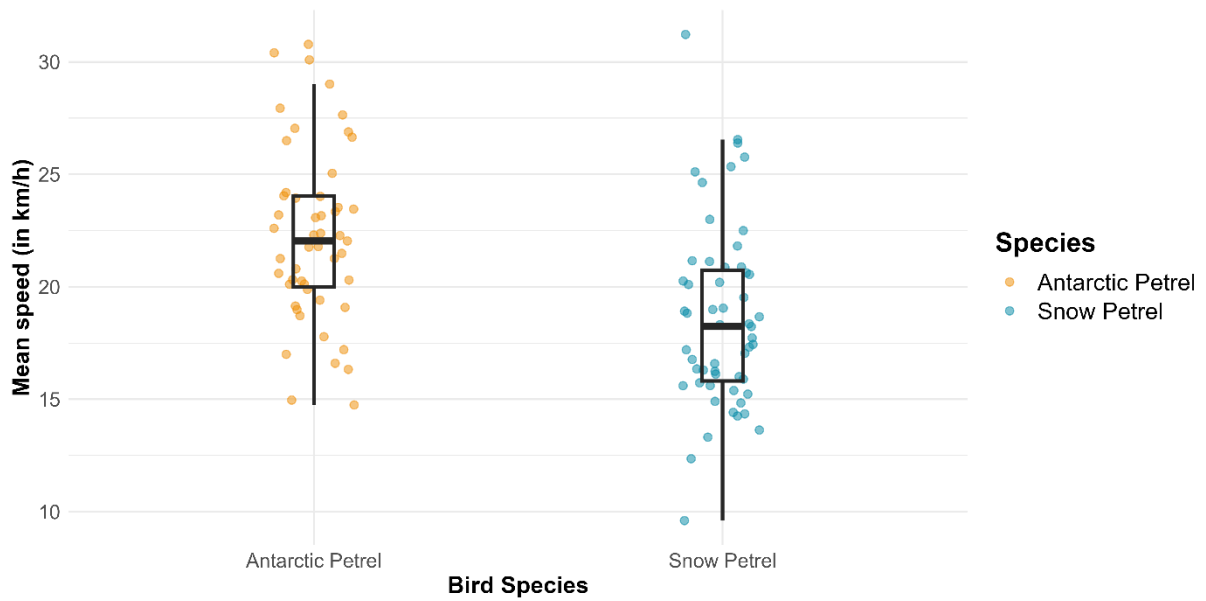
**Figure 4:** Mean speed traveled by individuals during their foraging trips per species. The colored point represents the values attributed to each trip, with jittering along the x-axis to increase visibility. The horizontal line is the median, the box represents the interquartile range (IQR), and the whiskers are the upper and lower quartile $\pm$ 1.95×IQR.

## 3.2. Overlap in foraging areas

After identifying the foraging behaviors from the HMM model, 7 869 locations were obtained for the Antarctic Petrels, and 8 082 for the Snow Petrels. The proportions of each state are shown in the appendix (Table SM4).

Antarctic Petrels generally foraged in regions further east and north as compared to Snow Petrels that remained closer to the coast, predominantly foraging to the west (Fig. 5).
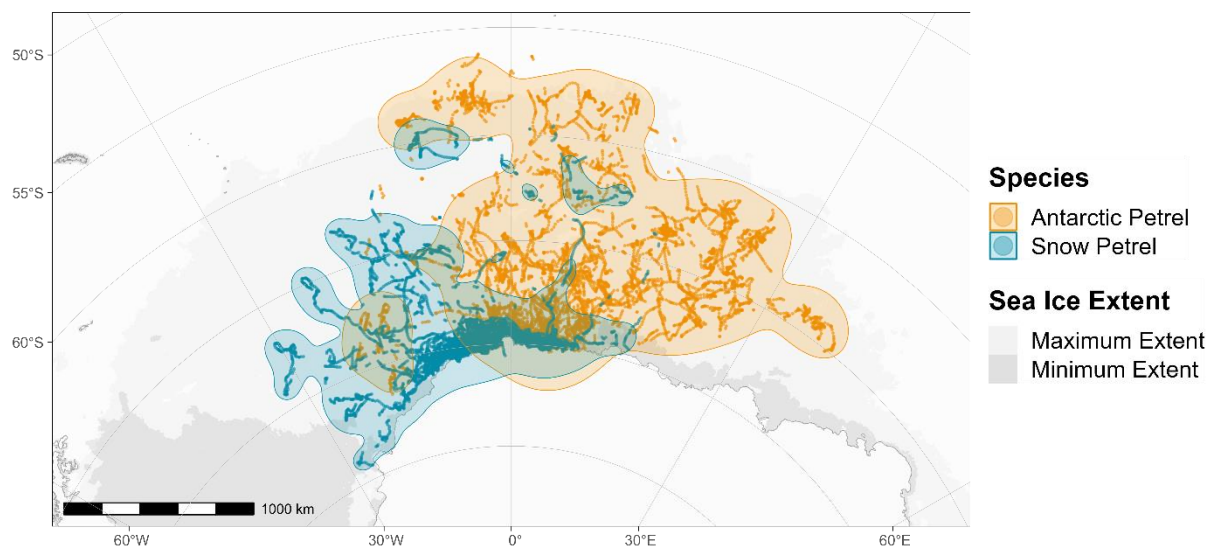
**Figure 5:** Foraging area of Antarctic and Snow Petrel during the whole breeding season. The figure shows the estimated foraging locations based on Hidden Markov Models and the 95% Utilization Distribution (orange for the Antarctic Petrels and blue for the Snow Petrels).

The HR overlap analysis showed that there was limited overlap between the foraging areas of the two species, with a mean of 12% (95th percentile: 5% - 18%) of the Antarctic Petrel's areas overlapped by the Snow Petrel's one throughout the breeding season, and 16% (95th percentile: 7% - 24%) of the Snow Petrel's area overlapped by the Antarctic Petrel's one (Fig. 6).

When considering all locations (and not only the foraging ones) the overlap was still small, with a mean of 18% (95th percentile: 10% - 25%) of the Antarctic Petrel's areas overlapped by the Snow Petrel's one, and 21% (95th percentile: 10% - 29%) for the Snow Petrel's area (Fig 6).

The same analyses were conducted to explore potential differences in spatial overlap during the incubation and chick-rearing periods. These analyses, illustrated in Fig. SM3 and SM4, showed no substantial variation in overlap between the two periods.
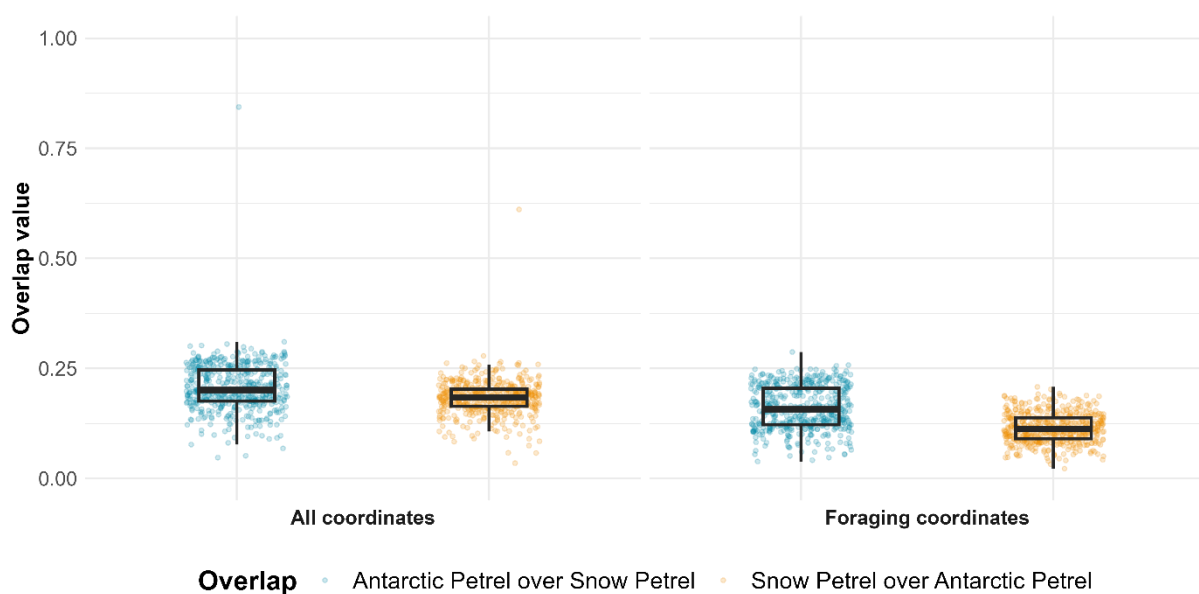


**Figure 6:** Overlap between areas used by Antarctic and Snow Petrels. Values are obtained with the "HR" method, considering all the locations or just the foraging ones. The colored points represent the values obtained after bootstrapping, with jittering along the x-axis to increase visibility. The horizontal line is the median, the box represents the interquartile range (IQR), and the whiskers are the upper and lower quartile ±1.95×IQR.

## 3.3. Sea-ice habitat use

The average sea-ice concentration at foraging locations did not differ significantly between species (Table 6; Fig. 7).
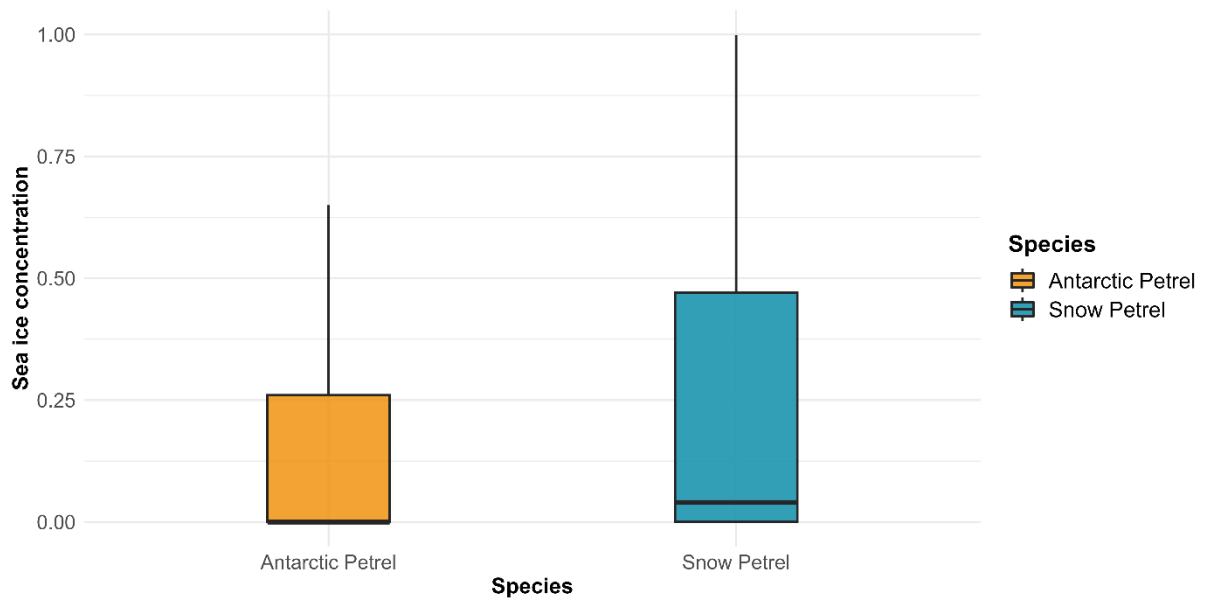
**Figure 7:** Boxplot of the sea-ice concentration at the foraging locations for Antarctic and Snow Petrels. The horizontal line is the median, the box represents the interquartile range (IQR), and the whiskers are the upper and lower quartile $\pm 1.95 \times$IQR.

However, when examining the zero-inflation component of the model, Snow Petrels were found to be less likely to forage in areas with zero sea-ice concentration compared to Antarctic Petrels (Table 6; Fig. 7). On average, Snow Petrels were 45% less likely to use zero ice concentration areas than Antarctic Petrels (Table 6).

Upon examining the overall sea-ice utilization by the birds, beyond just the foraging coordinates, results were similar. We observed no significant differences in sea-ice use when excluding the locations without sea-ice. However, when focusing exclusively on areas with zero sea-ice concentration, we found that Snow Petrels were 56% less likely to use zero ice concentration areas than Antarctic Petrels (Table 6).

**Table 6:** Species variation in the sea-ice concentration at Antarctic and Snow Petrel locations (all location and foraging locations only). Results represent the output of beta regression models (see Methods for details)

| Predictors | Ice concentration foraging | | Ice concentration all | |
|---|---|---|---|---|
| | Estimates | p | Estimates | p |
| Species [Snow Petrel] | 1.21 | 0.090 | 1.15 | 0.173 |
| **Zero-Inflated Model** | | | | |
| Species [Snow Petrel] | 0.45 | <0.001 | 0.56 | <0.001 |
| N | 106 $_{tripID}$ | | 106 $_{tripID}$ | |
| | 49 $_{BIRDID}$ | | 49 $_{birdID}$ | |

# 4. DISCUSSION

## 4.1. Difference in foraging trip characteristics

As predicted, Antarctic Petrels generally had longer foraging trips and traveled further away and at higher speeds than Snow Petrels. These differences can be explained by Antarctic Petrels being larger than Snow Petrels, with a similar wing load, allowing them to travel faster and further (Griffiths 1983, Marchant & Higgins 1990). However, some of these differences varied during the breeding season and during chick-rearing, Snow Petrels undertook longer trips than Antarctic Petrels. No obvious explanation for this pattern can be proposed, but one hypothesis could be that after incubation, once sea-ice has melted over large areas, the foraging areas accessible to Antarctic Petrels in their typical bearing of travel are closer than those available to Snow Petrels.

Significantly shorter trips were recorded when birds were caring for chicks, supporting our prediction. This change is likely due to the chicks' frequent need for nourishment, contrasting with the less demanding incubation period for nesting adults (Ito *et al.* 2010, Phillips *et al.* 2017).

Surprisingly, the reduction in the trips' duration and distance traveled during chick-rearing was not uniform between the species. Although a similar decline was anticipated for both species, given their comparable way of life, the decline was less pronounced for Snow Petrels. This may be explained by the already shorter trips undertaken by Snow Petrels during

incubation, limiting their ability to further reduce trip lengths during chick-rearing while still needing adequate time to reach and use foraging areas along the coast.

Regarding the bearing of foraging trips, Antarctic Petrels were found to travel more to the east than Snow Petrels both during incubation and chick-rearing. This already indicates a difference in the areas used by the two species for foraging.

## 4.2.  Spatial Segregation

A limited overlap in the foraging areas between Antarctic and Snow Petrels was revealed, both during incubation and chick-rearing. These results suggest spatial segregation between the two species, consistent with previous predictions and previous research on sympatrically breeding seabirds (Granroth-Wilding & Phillips 2019, Phillips *et al.* 2005, Pickett *et al.* 2018). The ecological similarities of the two species, including shared dietary preferences (Hoyo *et al.* 1992, Marchant & Higgins 1990), was indeed expected to lead to spatial segregation in order to avoid intense competition for resources. As previously suggested by the main bearing of the foraging trips, the foraging areas of the two species indicate that Antarctic Petrels generally use more northern and eastern areas, as compared to Snow Petrels that forage more to the west, and closer to the shore. Despite this general trend, some overlap was observed, indicating that part of the foraging areas was probably common for both species. When considering all locations at sea, and not only the foraging areas, the overlap was slightly larger but still <25%. This suggests that spatial segregation occurs across the entire range of their behavior (including transit and rest), not just within specific foraging zones.

Compared to previous studies on niche segregation among sympatrically breeding petrels, a mixed picture was found. Of the five studies examining two-dimensional spatial segregations in petrels, three reported segregations (Fromant *et al.* 2022, González-Solís *et al.* 2000, Navarro *et al.* 2013), while two did not (Delord *et al.* 2016, Reisinger *et al.* 2020).

The limited number of studies on this topic makes it difficult to properly understand these differences. More research is needed to gain a better understanding of the interspecific interactions among petrel species.

## 4.3. Difference in sea-ice use

Our results showed nuanced results about the sea-ice preferences of Snow and Antarctic Petrels. Contrary to the initial hypothesis, we found no significant difference in the preference for higher sea-ice concentrations between the two species over the overall season. This outcome was surprising, based on previous studies showing a high affinity of Snow Petrels towards areas of high sea-ice concentrations (Ainley *et al.* 1984, Hoyo *et al.* 1992). One potential explanation for this finding is the resolution at which sea-ice concentration was measured (Spreen *et al.* 2008). The 3 125 m grid cells used to describe sea-ice may be too coarse to detect subtle differences in habitat use, such as Antarctic Petrels favoring open water near the sea-ice edge and Snow Petrels utilizing cracks within the ice (Ainley *et al.* 1984, Hoyo *et al.* 1992). A finer resolution or an alternative measure, like the proximity to the sea-ice edge, might provide a more accurate reflection of each species' sea-ice preferences. However, despite the lack of significant differences in the use of higher sea-ice concentrations, the results revealed that Snow Petrels are significantly less likely to forage in zero sea-ice areas compared to Antarctic Petrels. This finding fits with known ecological behaviors of the species, suggesting that Antarctic Petrels are more inclined to forage in open water, while Snow Petrels exhibit a stronger association with sea-ice (Ainley *et al.* 1984). Additionally, sea-ice in Dronning Maud Land breaks down from the northeast to the southwest during the summer (Spreen *et al.* 2008). When examining the foraging areas of the two species, this pattern suggests that the Antarctic Petrel's areas are the first to experience a significant decrease in sea-ice. This observation adds depth to the differences in sea-ice use between the two species and could potentially explain the variations in their preferred foraging directions. Specifically, Antarctic Petrels tend to forage more northward and eastward, in areas that melt first, compared to Snow Petrels.

## 4.4. Study limitations and future considerations

This study focused primarily on spatial segregation, which provides only a partial view of the potential niche segregation of Antarctic and Snow Petrels. Future studies in this field would benefit from a comprehensive approach that incorporates multiple niche dimensions and environmental variables. More specifically, exploring both the spatial and nutritional dimensions simultaneously would provide valuable insights, particularly considering that

Antarctic Petrel's prey selection seems to vary with foraging location (Descamps *et al.* 2022). Previous studies suggest a form of dietary segregation, with Antarctic Petrels primarily focusing on krill, while Snow Petrels tend to favor fish (Ferretti *et al.* 2001, Lorentsen *et al.* 1998, Ridoux & Offredo 1989). Future research could investigate whether this dietary segregation is linked to their distinct foraging areas, where their preferred prey is potentially more accessible.

The limited number of direct dietary comparisons between these two species makes it challenging to determine whether their spatial segregation is due to distinct resource preferences or a strategy to minimize competition. Further research is essential to clarify the mechanisms behind the observed segregation and to enhance the understanding of the distribution and habitat use at sea for these petrel species.

## CONCLUSION

Breeding birds that share the same colony and similar lifestyles must develop strategies to mitigate the effects of competition, such as spatial segregation. This study revealed that, despite many similarities in their foraging behavior, Antarctic Petrels generally travel faster overall and cover greater distances than Snow Petrels during incubation. Surprisingly, their sea-ice use was found to be more alike than had been predicted. Yet, the minimal overlap in their foraging areas confirms that these species largely segregate to reduce competitive pressures, even though they likely share a similar fundamental niche.

In conclusion, these findings enhance the knowledge on the at-sea foraging behavior of these birds and identify critical foraging zones, such as the coastal areas favored by Snow Petrels during chick-rearing. Such insights are valuable for informing conservation efforts and guiding the design of future research on these species. The observed segregation between these two species may help in understanding the potentially different population trends observed at Svarthamaren. Indeed, the Antarctic Petrel population has been declining at Svarthamaren (Descamps *et al.* 2016; Descamps *et al.* 2023) while the Snow Petrel population seems to have been more stable (Descamps, *unpublished data*). A different use of the marine environment by these two species, as observed for the breeding season in this work, may explain part of these variations and should be investigated.

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# APPENDIX

**INCUBATION TRIPS**
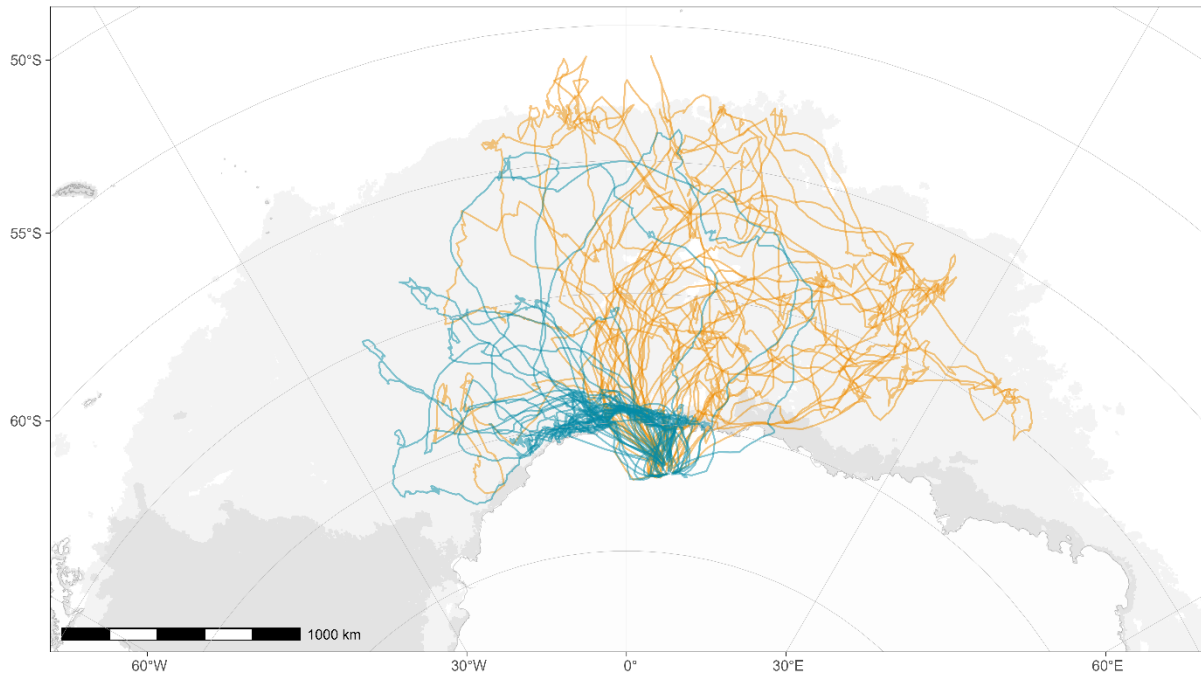


**CHICK-REARING TRIPS**
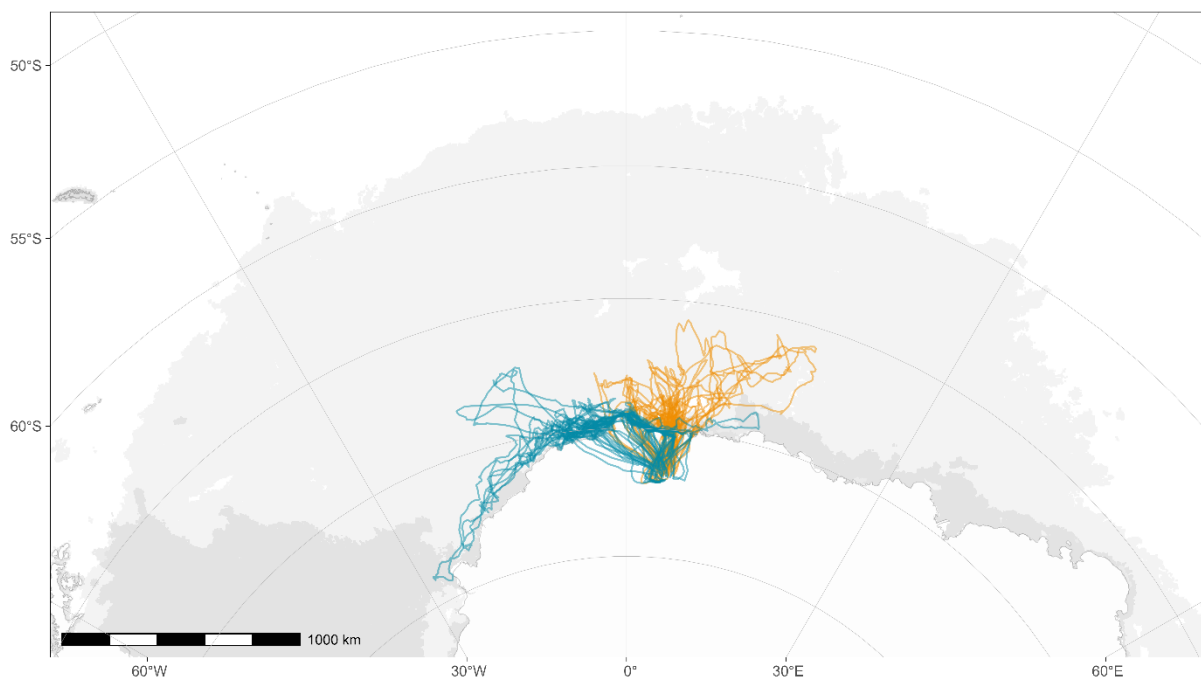


**Figure SM1:** Maps of the Antarctic and Snow Petrels foraging trips during incubation and chick-rearing. In orange are the Antarctic Petrels trips, and in blue the Snow Petrels ones.

**Table SM1:** Species and breeding status variation in foraging trip metrics. Results show the AIC and ΔAIC of all candidate models. Models with the lowest AIC are represented in bold. All models have the same random structure and column np represents the number of fixed parameters in each model.

| Metric | Model | AIC | ΔAIC | np |
|---|---|---|---|---|
| **Cumulative distance** | **~ SpeciesxStatus** | **1670.27** | **0.00** | **2** |
| | ~ Species+Status | 1738.92 | -68.65 | 2 |
| | ~ Status | 1768.12 | -97.84 | 1 |
| | ~ Species | 1772.64 | -102.37 | 1 |
| | ~ 1 | 1794.46 | -124.19 | 1 |
| **Maximal distance** | **~ SpeciesxStatus** | **1450.05** | **0.00** | **2** |
| | ~ Species+Status | 1487.85 | -37.80 | 2 |
| | ~ Status | 1505.72 | -55.66 | 1 |
| | ~ Species | 1522.28 | -72.23 | 1 |
| | ~ 1 | 1536.12 | -86.07 | 1 |
| **Duration** | **~ SpeciesxStatus** | **1056.02** | **0.00** | **2** |
| | ~ Species+Status | 1106.23 | -50.21 | 2 |
| | ~ Status | 1118.74 | -62.72 | 1 |
| | ~ Species | 1139.16 | -83.14 | 1 |
| | ~ 1 | 1148.27 | -92.25 | 1 |
| **Bearing** | **~ SpeciesxStatus** | **985.78** | **0.00** | **2** |
| | ~ Species+Status | 991.36 | 5.58 | 2 |
| | ~ Species | 996.04 | 10.25 | 1 |
| | ~ Status | 1035.92 | 50.14 | 1 |
| | ~ 1 | 1040.47 | 54.69 | 1 |
| **Mean speed** | **~ Species** | **594.01** | **0.00** | **1** |
| | ~Species+Status | 594.21 | 0.20 | 2 |
| | ~ SpeciesxStatus | 593.16 | 0.86 | 2 |
| | ~ Status | 607.24 | 13.23 | 1 |
| | ~ 1 | 607.28 | 13.27 | 0 |

**Table SM2:** Correlation between the five foraging trip metrics (both species combined). The correlations are similar when considering each species separately.
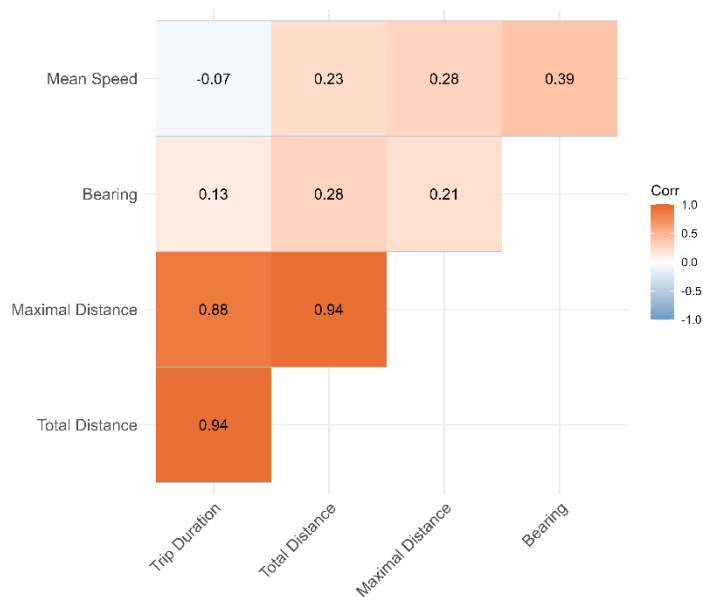


**Table SM3***:* Species and breeding status variation in the sea-ice concentration at Antarctic and Snow Petrel foraging locations. Results represent the AIC and ΔAIC scores from Zero inflated beta regression mixed models (see details in Methods). Models with the lowest AIC are represented in bold. All models have the same random structure and column np represents the number of fixed parameters in each model.

| Models | AIC | ΔAIC | np |
|---|---|---|---|
| **~ Species** | **18640.22** | **0.00** | **1** |
| ~1 | 18641.13 | 0.91 | 1 |
| ~ Species*Status | 18641.51 | 1.29 | 2 |
| ~ Species+Status | 18642.22 | 2.00 | 2 |
| ~ Status | 18643.13 | 2.91 | 1 |

**Table SM4:** Number of locations for each state and their proportions for Antarctic (AP) and Snow Petrels (SP).

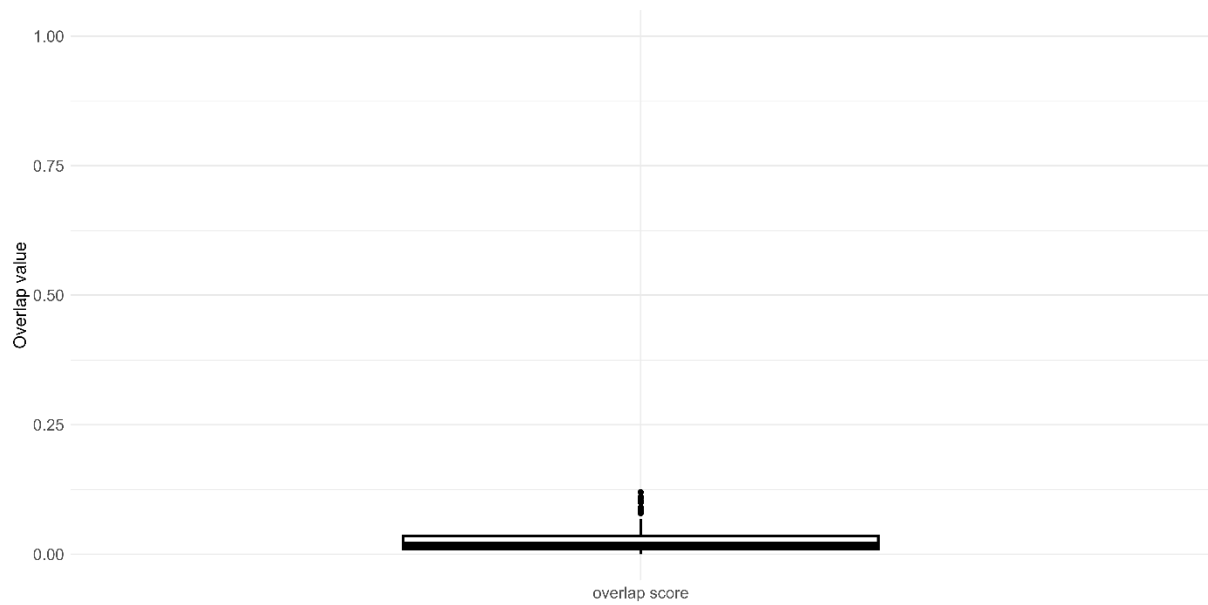| States | Number.locations.AP | Proportion.AP | Number.locations.SP | Proportion.SP |
|---|---|---|---|---|
| **Rest** | 3,074 | 0.22 | 4,088 | 0.27 |
| **Fine foraging** | 3,896 | 0.28 | 4,303 | 0.28 |
| **Coarse foraging** | 3,973 | 0.28 | 3,779 | 0.25 |
| **Slow transit** | 2,441 | 0.17 | 2,181 | 0.14 |
| **Fast transit** | 630 | 0.04 | 931 | 0.06 |

**Figure SM2:** Boxplots of the overlap scores obtained with the Utilization Distribution Overlap Index method after 500 iterations (based on bootstrap), between Antarctic and Snow Petrel foraging areas. It describes the probability of finding two birds of different species at the same coordinates (Fieberg & Kochanny 2005), 0 meaning no overlap and 1 a total overlap. The vertical black line is the median, the box represents the interquartile range (IQR), the whiskers are the upper/ lower quartile ± 1.95×IQR and the points are the outlier values.

**Incubation**
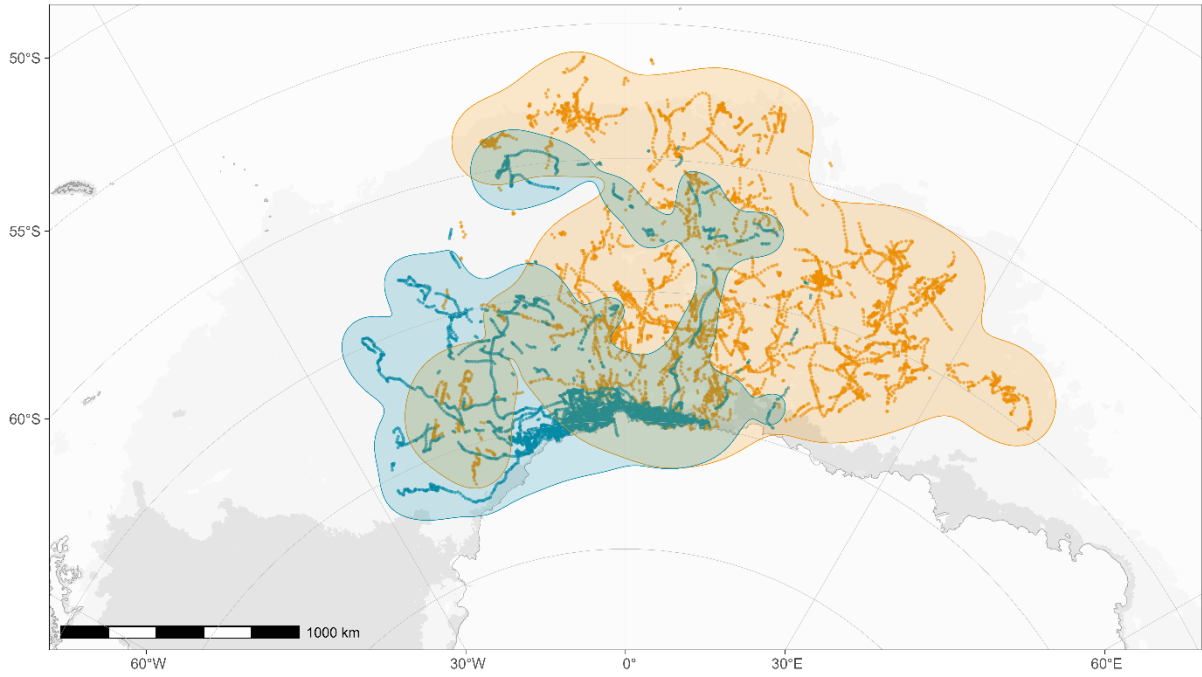


**Chick-rearing**
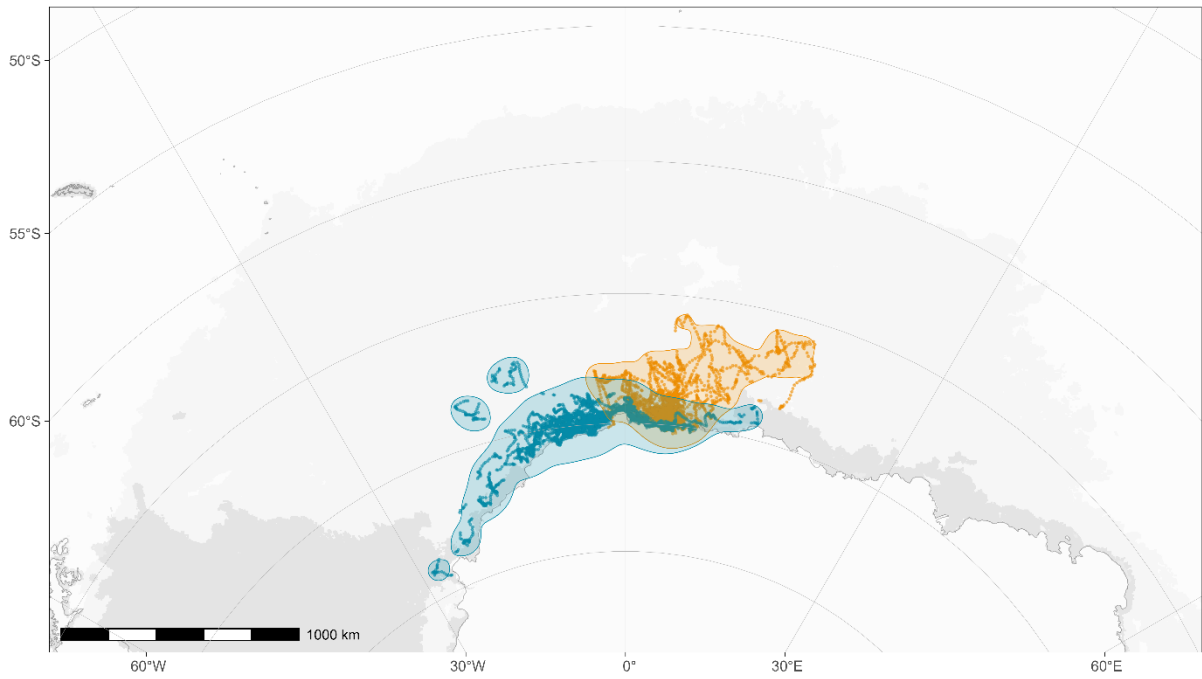


**Sea Ice Extent** — Maximum Extent — Minimum Extent **Species** — Antarctic Petrel — Snow Petrel

**Figure SM3:** Foraging areas (95% Utilization Distribution) of Antarctic and Snow Petrel during incubation and chick-rearing.
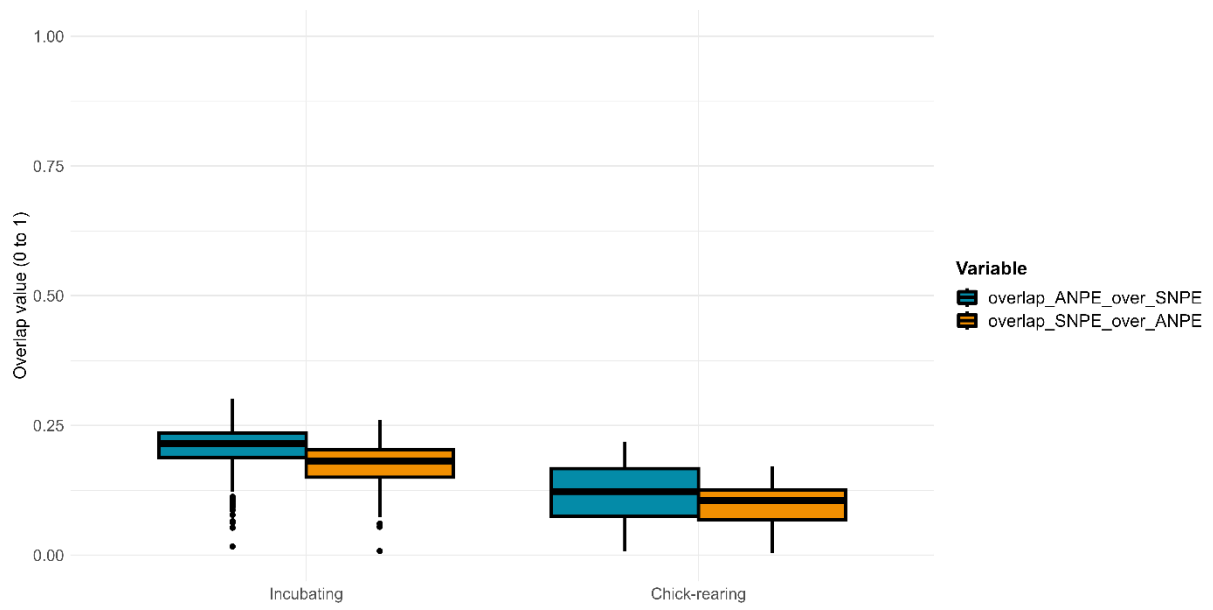
**Figure SM4:** Boxplot of the overlap scores obtained after bootstrap (with the HR method) for Antarctic and Snow Petrel during incubation and chick-rearing. The horizontal line is the median, the box represents the interquartile range (IQR), the whiskers are the upper and lower quartile ± 1.95×IQR and the points are the outlier values.