



Using telemetry data and the sea ice satellite record to identify vulnerabilities in critical moult habitat for emperor penguins in West Antarctica

Philip N. Trathan¹ · Barbara Wienecke² · Andrew Fleming¹ · Louise Ireland¹

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Abstract

We tracked adult emperor penguins from Rothschild Island, west Antarctic Peninsula in 2015/2016 during a summer with extensive sea ice of long duration, contrasting with past years of reduced sea ice extent associated with the recent, rapid, warming trend across the region. We fitted ARGOS PTT devices to penguins of unknown breeding status. Of 33 penguins tracked, nine returned to the colony, presumably to provision offspring. Their foraging trips lasted 9.6 ± 3.7 days, with maximum distances of 75 ± 45 km from the colony within coastal waters. Also, 18 instruments transmitted until the initiation of the annual moult. Penguins travelled at ~ 2.3 km h⁻¹ before slowing for moult. Post-moult, some devices continued to transmit, with speeds of ~ 0.8 km h⁻¹, plausibly due to ice drift, which is rapid in this region. Penguins remained within the seasonal sea ice throughout, staying within 100 km of land, and generally within 5 to 10 km of features (open water, polynyas, leads, icebergs) that offered potential access to the ocean. Penguins were unlikely to have been constrained by the extensive sea ice habitat in 2015/2016. Similar habitats would also have been available in most years of the satellite record (since 1979); however, the moult locations in 2015/2016 would not have been available in many years, and penguins would have needed to find alternative moult locations during some years. Despite uncertainties, the moult period is a critical time for emperor penguins, particularly as sea ice declines, potentially affecting adult survival.

Keywords Emperor penguins · West Antarctic Peninsula · Rothschild Island · ARGOS telemetry · Foraging · Moult

Introduction

Emperor penguins (*Aptenodytes forsteri*) are highly dependent upon sea ice during much of their annual cycle (Trathan et al. 2020) and for most of their adult life. Almost all breeding sites are situated on land-fast sea ice, where the most important physical characteristics appear to be ice stability, access to fresh snow, possibly open water (Kooyman 1993), and possibly shelter from the wind (Zitterbart et al. 2011, 2014). Similarly, known moult sites also appear to be restricted to consolidated or perennially

persistent pack ice, or fast ice (Kooyman et al. 2000; Wienecke et al. 2004; Zimmer et al. 2008). Many emperor penguin colonies occur near polynyas (areas of persistent open water, or thin sea ice) within the larger-scale ice field (Massom et al. 1998, 2009) or close to “flaw leads” that form at the junction of coastal fast ice and offshore pack ice. Depending on the size and persistence, these areas of open water may provide foraging opportunities, at least partially. Emperor penguin diet has mainly been studied during chick rearing, when it is dominated by prey species that are also intimately linked with sea ice, including fish (particularly Antarctic silverfish, *Pleuragramma antarcticum*), crustaceans (mainly Antarctic krill, *Euphausia superba*) and squid (particularly the arrow squid, *Psychroteuthis glacialis*, and the Antarctic neosquid, *Alluroteuthis antarcticus*); see Offredo and Ridoux (1986); Klages (1989); Ainley et al. (1992); Wienecke and Robertson (1997); Cherel and Kooyman (1998); Kooyman et al. (2004); Cherel (2008); and review by Ratcliffe and Trathan (2012). However, juveniles and non-breeding penguins

✉ Philip N. Trathan
pnt@bas.ac.uk

¹ British Antarctic Survey, High Cross, Madingley Road, Cambridge CB3 0ET, UK

² Department of Climate Change, Energy, the Environment and Water, Australian Antarctic Program, 203 Channel Highway, Kingston, TAS 7050, Australia

sometimes forage far from the continent, beyond the sea ice zone (Kooyman et al. 1996; Kooyman and Ponganis 2008; Wienecke et al. 2010; Thiebot et al. 2013; Goetz et al. 2018; Labrousse et al. 2019).

In contrast to the large-scale decreases in sea ice extent observed in the Arctic over the satellite era (1979 to 2023), seasonal Antarctic sea ice extent has remained relatively consistent (nsidc.org; last accessed 13 March 2024), with even increased sea ice extent until 2015 (Comiso et al. 2017). Only since 2016 has Antarctic sea ice shown evidence of a circumpolar decrease in extent and area (Turner et al. 2022). It is currently unknown whether this may reverse in time, like previous anomalies, or is indicative of long-term change in Antarctic sea ice conditions. Only along the Antarctic Peninsula has there been a persistent decreasing trend, with later sea ice advance in Autumn and earlier sea ice retreat in Spring, giving a reduced sea ice duration trend of > 3 days per year over the period 1979/1980 to 2010/2011 (Stammerjohn et al. 2012; Ducklow et al. 2013).

For emperor penguins breeding at the west Antarctic Peninsula, the reduction in sea ice habitat is likely to have important implications. Currently, six small colonies are known to exist along the west Antarctic Peninsula. One of these, at Emperor Island, Dion Islands, Marguerite Bay, was one of the earliest reported colonies anywhere in the Antarctic (Stonehouse 1952) and has always been small in size. The colony at Emperor Island persisted at least until 2001 (Trathan et al. 2011). Although a few individuals have subsequently been sighted at the colony (Hart 2016), it is now probably functionally extinct. This has been attributed to the substantial warming trend (Vaughan et al. 2001) along the west Antarctic Peninsula, with associated reductions in sea ice area and extent (Stammerjohn et al. 2012).

Altered sea ice habitats may have important consequences for food webs, including changes in food web composition and species abundance (Constable et al. 2014). Even though emperor penguins are generalist feeders (Trathan et al. 2020), energy dense prey remain vital for maintaining their ability to endure and breed.

Beyond the immediate loss of breeding habitat, or altered foraging opportunities, reduced sea ice extent may have also led to other risks (Trathan et al. 2011). These include altered weather patterns, increased ocean swell when sea ice is insufficient to dampen wave action and loss of the protective sea ice barrier that excludes other marine vertebrates, including giant petrels (*Macronectes giganteus*) that are known to take chicks, or Antarctic fur seal (*Arctocephalus gazella*) whose populations have recovered from historical exploitation. Fur seals may increase levels of disturbance at breeding sites as male seals migrate southwards after breeding (Lowther et al. 2020). All of these have the potential to affect breeding activities negatively, possibly leading to colony decline in the long term.

As of 2015, apart from Emperor Island, all other breeding sites along the west Antarctic Peninsula were only known from satellite observations. Known sites include Rothschild Island (LaRue et al. 2015), Verdi Inlet (Fretwell and Trathan 2021), Smyley Island (Fretwell and Trathan 2009), Bryan Coast (LaRue et al. 2015), and Pfrogner Point (Fretwell and Trathan 2021). We selected the most northerly of these sites, Rothschild Island, at the western side of the Antarctic Peninsula for this telemetry study.

No telemetry data for emperor penguins have ever been collected from colonies in West Antarctica. We investigated the location of the study colony by aerial reconnaissance to determine whether it was suitable for tracking adult penguins in order to determine foraging grounds at the end of the breeding season in 2015/2016 and also possible moult locations if telemetry devices continued to provide information. A secondary objective was to compare foraging and moult areas with the historical record of sea ice. Finally, we conducted a colony-wide census of chicks to gain some measure of the size of this colony.

Materials and methods

Our study took place from 12 November to 1 December 2015, at the emperor penguin colony at Rothschild Island (69° 30' S, 72° 18' W; Fig. 1) located on sea ice < 1 km from the eastern coastline of the island in Lazarev Bay. This rectangular bay separates Rothschild Island from the much larger Alexander Island, bounded on the south side by the Wilkins Ice Shelf, whilst the mouth of the bay opens northwards onto the shelf waters of the west Antarctic Peninsula (Fig. 1). In 2015/2016, Lazarev Bay was covered in fast ice trapping hundreds of small ice bergs and bergy bits some of which, at times, provided some shelter for the colony. We accessed the fast ice via a steep snow bridge from the Rothschild ice piedmont. In November 2015, the edge of the fast ice west of the colony was about 75 km away (see SM Fig. 1).

Animal capture and instrumentation

The joint Cambridge University/British Antarctic Survey Animal Ethics Committee and the Australian Antarctic Division Animal Ethics Committee approved all animal handling procedures used in this study.

To capture adult emperor penguins, we approached on foot and captured them using a long-handled crook. We only captured individuals on their return to, or departure from, the colony to minimise disturbance to other animals; as such, we could not determine individual breeding status. We caught 33 adult penguins and pulled a canvas bag over their head, keeping the head free so that the individual

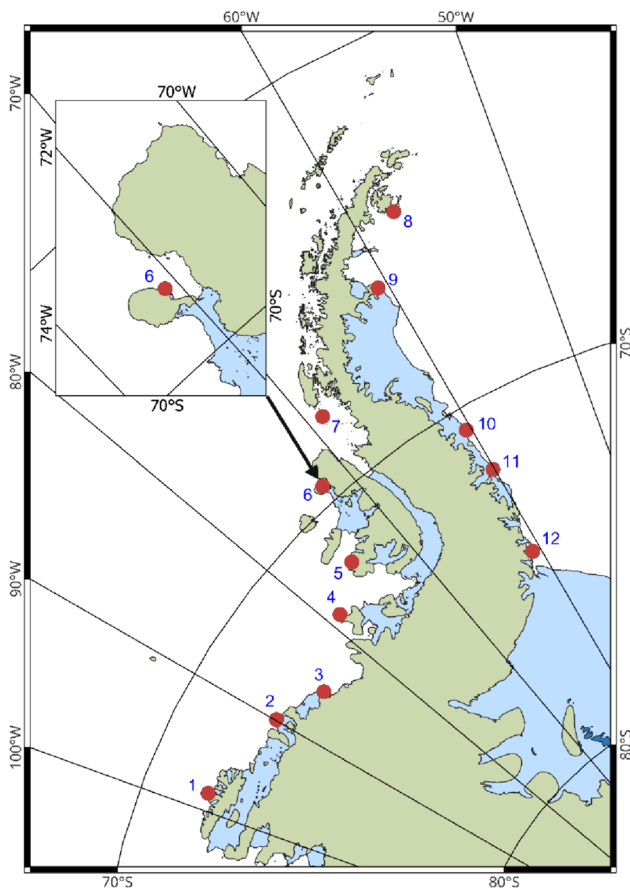


Fig. 1 Locations of emperor penguin colonies in the Bellingshausen Sea and on the Antarctic Peninsula; 1—Noville Peninsula, 2—Pfrogner Point, 3—Bryan Coast, 4—Smyley Island, 5—Verdi Inlet, 6—Rothschild Island, 7—Emperor Island, 8—Snow Hill Island, 9—Larsen Ice Shelf (Jason Peninsula), 10—Dolleman Island, 11—Cape Darlington, and 12—Smith Peninsula. Our study colony was at Rothschild Island (6, see inset); the colony at Emperor Island (7, Dion Islands) is thought to be no longer extant

could breathe; the bag minimised flipper movements and controlled the penguin during subsequent handling. We weighed each penguin to the nearest 0.5 kg using a suspended mechanical scale and attached either a Wildlife Computers ($n = 15$) (model SPOT-275 rated to 2000 m; 90 g; $86 \times 17 \times 18$ mm) or Sirtrack ($n = 18$) (Kiwisat K2G 273A rated to over 500 m; 95 g; $78 \times 43 \times 27$ mm) satellite telemetry (ARGOS PTT) device to each individual. The Wildlife Computers tags were programmed to transmit at 60 s frequency, whilst the Kiwisat tags transmitted every 90 s. We attached devices on the dorsal mid-back of each penguin using Loctite 401 quick-setting glue and two plastic cold-resistant cable ties, which we sealed with glue. After release, we observed each penguin for as long as possible but did not detect any unusual behaviour. Outbound birds continued on their journey and inbound birds joined the colony. None tried to peck at the attached

instrument. Capture, instrumentation, and release generally took less than 10 min per penguin.

Given our limited time in the field, we recognised that we would not be able to recapture instrumented penguins; hence, we did not mark individuals.

The deployment of ARGOS PTT devices, or any externally fitted device, is likely to have consequences for penguins, as devices will inevitably lead to increased hydrodynamic drag. Such increases may become important for longer-term deployments. We therefore attempted to minimise any such effect by careful location and alignment of devices on each penguin and by only selecting penguins in good condition. We followed practices developed by others (e.g. Wienecke et al. 2004).

Tracking data

To prolong battery life, the PTTs were programmed to switch on when wet ('wet' mode) and so only transmitted positional data, whilst the penguins were at sea; when hauled out, devices transmit at a lower frequency. The deployment period ended when the penguins moulted approximately 2 or 3 months later, resulting in the PTT falling off. Transmissions mostly ceased, although we found that a small number of devices continued to transmit data after the end of the estimated moult period (see SM Table 1).

All PTT location data were analysed using R version 3.5.1 (R Core Team 2018). Initially, fixes that would have required an average cruising speed of $> 2.2 \text{ m s}^{-1}$ (Sato et al. 2005, 2010) were removed using *speedfilter* (R package *trip* v1.6.0; Sumner et al. 2009). We then used *crwMLE* (R package *crawl* v2.2.1; Johnson et al. 2008; Johnson and London 2018) to fit continuous time correlated random walk models (all of which converged) and interpolated tracks at 5-min intervals using *crwPredict*. Telemetry data are often incomplete or imprecise, as such these models allow for uncertainty in location. Location data from the 5-min interpolated tracks were used for all subsequent analyses. Characteristics of each penguin tracked are given in SM Table 1. The tracking data cover the period from deployment until the time when the penguin's annual moult was underway, although some tags ceased transmitting earlier.

Sea ice data

In the 2015/2016 season, sea ice conditions were anomalously extensive, compared with the years immediately prior. Visual observation during the air transfer from Rothera to Rothschild Island revealed that most of the southern part of Marguerite Bay was still covered in fast ice, with extensive fast ice to the northwest of both Alexander Island and Rothschild Island (see SM Fig. 1). As part of our analyses, we compared various satellite-derived sea ice datasets with

our telemetry data to explore how emperor penguins utilised their habitat.

Habitat use at the end of the breeding season in 2015/2016

For each 5-min interpolated penguin track (output from *crwPredict*), we accessed satellite imagery (see below) to explore contemporaneous sea ice characteristics at each track point. For each point or cluster of points (where these fell within a given time window; see below), we measured the shortest distance to land, to the marginal sea ice zone (< 15% of sea surface is ice covered; Worby et al. 1998), and to open water.

To measure distance to land, we used the high-resolution coastline from the SCAR Antarctic Digital Database (www.add.scar.org/; 12 May 2021, version 7.4). We ignored sea stacks, rocks, or small offshore islands that probably would not be accessible as haul-out sites.

To measure distance to the pack ice edge, we used ice concentration data from the Advanced Microwave Scanning Radiometer 2 (AMSR2; earthdata.nasa.gov/earth-observation-data/near-real-time/download-nrt-data/amsr2-nrt; last accessed 01 August 2023) to provide a daily sea ice edge matching the time stamp of each point or centroid. The AMSR2 images used had a spatial resolution of 6.25 km.

To measure distance to open water, we used satellite synthetic aperture radar (SAR) imagery from Sentinel-1 (sentinel.esa.int/web/sentinel/home; last accessed 01 August 2023; Copernicus Sentinel data 2023). This 40-m resolution imagery has a high repeat frequency with no impacts from cloud cover. We matched each track point to an image acquired within a fixed time window of the time stamp for each track point. We examined closeness in time of track time stamp with SAR image acquisition using different time windows of 2 h, 4 h, and 12 h to determine the best concurrency. Matching track points with a time window of 2 h (1 h either side of the track point time stamp) provided good coverage of 320 individual penguin ‘events’ within the tracking data and covered 29 out of the 33 penguins. Each penguin ‘event’ contained at least one or many track points for the given time window. Therefore, to measure the distance of a penguin to the nearest point where we postulated open water to exist, we calculated a mid-point for clusters. For each track point, or cluster mid-point, we measured the distance to open water (open water, polynya, lead, proximity to an iceberg > 120 m, or to land where tide cracks may occur). Three independent analysts conferred where discrepancies occurred to avoid subjective interpretation. The average correlation between analysts was 0.71; most discrepancies occurred where it was not possible to identify habitat features with certainty due to the quality of the images. For example, features, including open water, may be present, but

identification may not be possible if features fall below the limits of the image spatial resolution or due to the presence of speckle in SAR imagery which degrades interpretability. In some situations it was not possible to identify any areas of open water or tide cracks, although these may have existed where ice floes meet (e.g. Fig. 2). Floes can freeze together to form a nearly continuous sea ice surface, particularly in areas where sea ice concentration is high. In SAR imagery (Fig. 2), the lighter areas possibly indicate pressure ridges that form where ice floes bump together, whilst the darker grey areas indicate relatively flat surfaces. The thickness of sea ice varies locally but cannot be discerned directly from satellite imagery.

Habitat use post-breeding and during moult in 2015/2016

For each 5-min interpolated penguin track (output from *crwPredict*), three analysts undertaking independent assessments determined the time at which each penguin stopped moving over extended distances, presumably to moult. Some devices ceased transmission prior to the moult period, presumably because the ARGOS PTT device failed, or was lost from the penguin. During moult, emperor penguins may move short distances (for example, to access and eat fresh snow), so the location of moult most likely comprises an

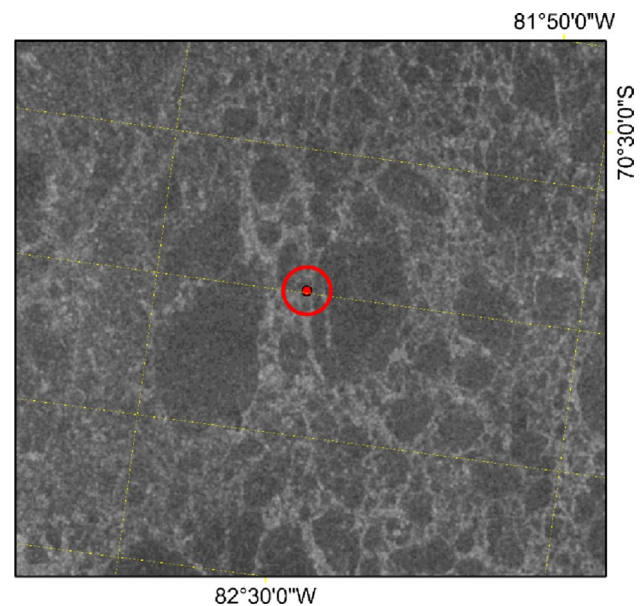


Fig. 2 Example of a penguin tracking centroid (circled in red) with no evidence of open water, but where cracks in the pack ice may exist. The graticule is shown with intervals of 10 min of longitude and latitude. Image S1A_EW_GRDM_1SSH_20151222T020838_10 B7_S_1.tif captured on 22 December 2015 at 02:08 UTC. Note that ice floes freeze together, and the lighter areas possibly indicate pressure ridges that form where ice floes bump together, whilst grey areas indicate relatively flat surfaces. The thickness of ice is variable

area rather than a point feature. Further, pack ice drifts with the ocean currents, so moult locations may appear to shift.

To determine moult locations, visual inspection of travel speeds identified relatively stationary periods across a span of dates. We determined that the initiation of moult for individual penguins ranged from 9 December 2015 to 20 January 2016.

Habitat availability based on the historical satellite record

To determine how the 5-min interpolated penguin tracks (output from *crwPredict*) compared with the 15% ice edge in each month (November through February) for the years between 1978 and 2022, we accessed imagery from the NOAA archive of sea ice extent for the west Antarctic Peninsula (https://noaadata.apps.nsidc.org/NOAA/G02135/south/monthly/shapefiles/shp_extent/; last accessed 01 August 2023). NOAA sea ice maps provide an indication of sea ice cover, albeit at a scale (25 × 25 km) that is relatively coarse compared with ARGOS telemetry data and with the size of potential moult areas. Nevertheless, NOAA sea ice maps do provide an indication of how habitat has changed over the duration of the satellite record.

For the late-breeding season (November) in each year of the archive, we scored the count of the penguin tracks that would have fallen completely within the sea ice extent for a given year and then plotted the time series.

For the post-breeding and moult period (December, January and February) in each year of the archive, we categorised four potential moult areas to identify whether each occurred within: full sea ice cover (score 3); partial sea ice cover (score 2); or no sea ice cover (score 1). We then averaged the scores from the four locations for each month and year combination and plotted the time series.

Results

Chick census

A photographic count of 714 live chicks was made at the Rothschild Island colony on 16 November 2015. At this time, the chicks were spread out and could easily be counted. None had commenced the final moult, and only two dead chicks were sighted. The colony was first sighted from the air on a reconnaissance flight on 5 November 2015. Subsequent to that date, it had moved by about 1 km northwards when we first accessed it on the ice, and continued to do so. Thus, chicks that had died previously were south of the location where the count took place, and were likely buried under snow.

Satellite tracking

We report the primary properties for each ARGOS PTT deployment as well as the mapped outputs from *crwPredict* for each penguin track (Fig. 3; SM Table 1). On average, the devices continued to transmit for 77.7 days (range 6.4–165.2 days). The majority of penguins ($n = 24$) did not return to the colony after tag deployment, suggesting that most penguins were non-breeders or failed breeders. However, nine penguins returned to the colony after one or more complete foraging trips, presumably feeding offspring (Table 1). Further, 18 tags continued to transmit until the start of the annual moult (Table 2); the average tracking period prior to moult was 46.0 days (range 14.0–66.8 days). We assumed a penguin had commenced its moult when the bird ceased directional travel, slowed, and remained within a limited area. However, given ice movement and uncertainty in tag location, moult locations covered > 20 km. Eight out of 18 devices continued to transmit and resumed directional travel after the presumed moult period had ended, plausibly because they continued to transmit from drifting pack ice. One penguin showed no evidence of slowing to moult and continued to travel until the end of the study. The last recorded positions were on 26 April 2016 when data collection was terminated; at this date, five (possibly six) instruments were still transmitting (SM Table 1).

Sea ice information

During the summer of 2015/2016, based on satellite imagery (SM Fig. 1) and observations during reconnaissance flights, it was evident that the fast ice area extended from the northern coast of Alexander Island some 33 km north to ~68° 31' S, extending south via Charcot Island (69° 57' S, 75° 10' W) to the western side of Latady Island (70° 55' S, 75° 10' W) covering an area of about 21,000 km². In late November 2015, the fast ice extended approximately 75 km west of Rothschild Island, and the pack ice zone was roughly 250 km wide. Several areas of open water existed near the coasts west of Charcot and Latady islands and farther south southwest of Smyley Island. Pack ice-filled Bach Inlet south of Latady Island and the Ronne Entrance. From December 2015 to February 2016, the band of pack ice narrowed, and near the coast, the areas of open water increased.

Habitat use at the end of the breeding season in 2015/2016

All penguins stayed relatively close to land, mainly within 100 km or less of the coast (Fig. 4a). They remained almost exclusively well within the pack ice zone throughout the duration of the study, moving only occasionally towards the ice edge (Fig. 4b). At fine scales (< 5 km), the interpolated

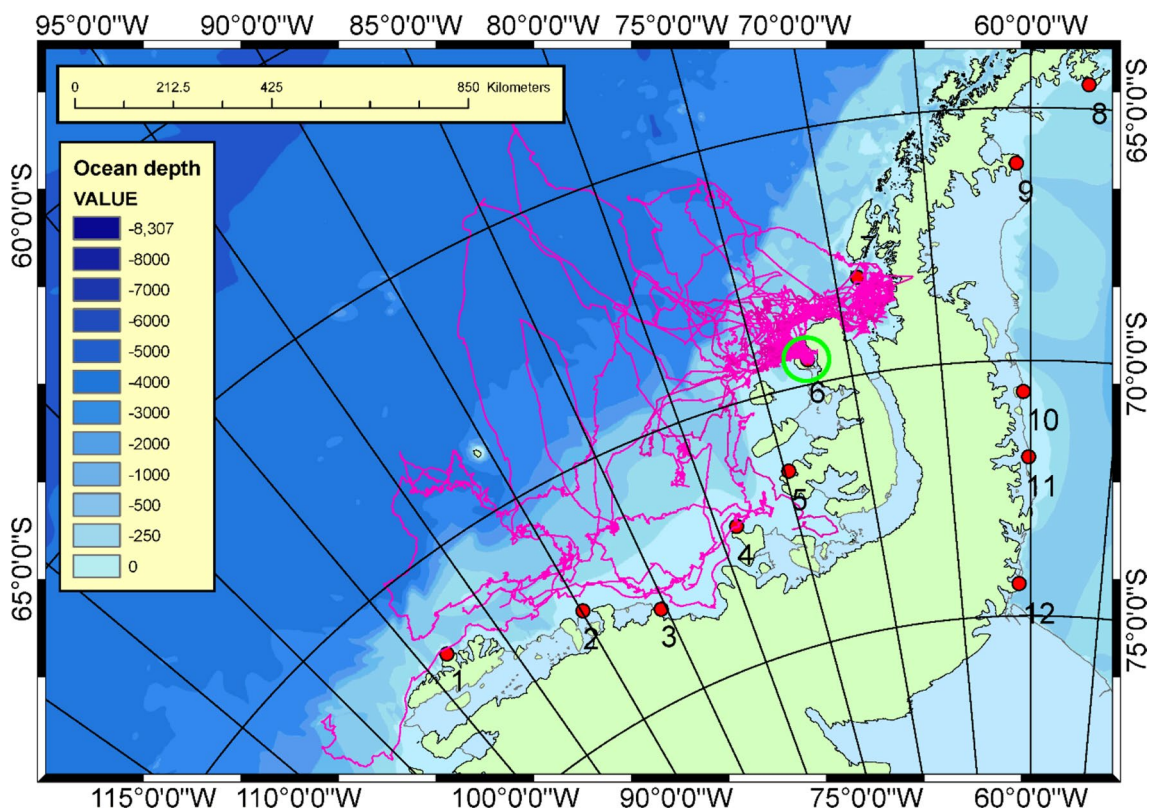


Fig. 3 Plot showing the locations of emperor penguin colonies on the Antarctic Peninsula, together with raw tracking data from 33 ARGOS devices deployed at Rothschild Island (circled in green). Clockwise, the emperor penguin colonies are 1—Noville Peninsula, 2—Pfrogner Point, 3—Bryan Coast, 4—Smyley Island, 5—Verdi Inlet, 6—Roths-

child Island, 7—Dion Islands (Emperor Island) functionally no longer extant, 8—Snow Hill Island, 9—Larsen Ice Shelf (Jason Peninsula), 10—Dolleman Island, 11—Cape Darlington, and 12—Smith Peninsula

penguin track points (or clusters) generally occurred close to features evident in the imagery, such as open water (9%), polynyas (6%), leads (49%), icebergs (29%), or land (3%) (Fig. 4c). Based on observations of penguins at the study colony, we assumed that tide cracks near icebergs or near land may allow access to and from the ocean beneath. A small proportion (<3%) of locations were > 10 km from any clearly detectable feature (Fig. 4c). In these situations, the sea ice was generally smooth, but with evident discontinuities that could reflect stress in the ice or ice floe margins (Fig. 2). These stress lines may reflect pressure in the ice, with formation of ridges, or areas of weakness that might afford access to the ocean beneath; however, the resolution of the SAR imagery was insufficient to determine whether either was the case.

The nine penguins that made return foraging trips (Fig. 5; Table 1) stayed close to shore, remaining within ~75 km of the coast. Penguins provisioning offspring are more constrained with regard to the distances they can travel, than are non-breeders or failed breeders, and presumably focussed their foraging efforts in the nearest predictable and profitable areas.

Habitat use post-breeding and during moult in 2015/2016

Of the 33 tracked penguins, 18 carried PTT devices that transmitted continuously until the time that the moult period was thought likely to commence (Fig. 6; Table 2). From the time of deployment until the time when the movement of individuals slowed, penguins travelled on average at speeds of ~2.3 km h⁻¹ (individual average speeds ranged from 0.9 to 3.8 km h⁻¹).

Adults moulted in areas ranging from Marguerite Bay (68° 30' S, 68° 30' W) to Pfrogner Point (72° 37' S, 89° 35' W). Moult locations were generally on sea ice offshore (up to 250 km from the coast) over the continental shelf where water depths were 250 m or less, although a few locations were over deeper water. In the 2015/2016 summer, the seasonal sea ice was extensive but comprised mainly mobile pack ice.

Some tags continued transmitting beyond the moult but moved very slowly. Presumably these were lost onto sea ice which was then carried by the East Wind Drift (e.g. Kwok

Table 1 Characteristics of completed foraging trips of tracked adult emperor penguins that returned to the colony

PTT_id	Foraging trip id	Furthest distance (km)	Trip distance (km)	Trip speed (km h ⁻¹)	Trip duration (d)
98534	1	194.6	1492.1	3.5	17.8
98534	2	121.7	1021.1	3.6	11.8
98534	3	49.4	371.9	2.9	5.3
98534	4	118.8	1194.8	3.2	15.6
130999	1	63.2	228.5	1.2	7.9
130999	2	65.5	235.8	1.2	8.2
130999	3	100.3	466.3	1.6	12.1
131433	1	68.4	282.9	1.1	10.7
131433	2	80.9	320.3	1.2	11.1
131433	3	77.6	295.0	1.3	9.5
131429	1	12.9	108.2	0.5	9.0
98536	1	84.4	351.6	1.4	10.5
131002	1	22.5	80.4	0.5	6.7
131003	1	82.8	239.3	1.2	8.3
131431	1	34.8	98.8	1.0	4.1
150631	1	28.3	111.9	1.0	4.7
Mean ±SD		75 ± 45	431 ± 422	1.6 ± 1.0	9.6 ± 3.7
Median		73	289	1.2	9

Each trip id reports the properties of an individual foraging trip

Table 2 Deployment characteristics for adult emperor penguins tracked until moult

PTT_id	Start latitude	Start longitude	Moult latitude	Moult longitude	Tracking Start date	Moult Start date	Tracking period before moult (d)	Device active after moult
98530	- 69.49	- 72.24	- 69.47	- 74.71	14/11/2015	12/12/2015	27.3	Y
98531	- 69.50	- 72.26	- 68.98	- 68.30	14/11/2015	29/12/2015	45.2	N
98532	- 69.50	- 72.27	- 71.11	- 89.54	13/11/2015	08/01/2016	56.2	Y
98533	- 69.52	- 72.23	- 69.13	- 68.84	13/11/2015	16/01/2016	64.0	N
98534	- 69.52	- 72.33	- 68.87	- 70.17	15/11/2015	08/01/2016	53.9	N
98535	- 69.51	- 72.29	- 69.05	- 69.00	13/11/2015	07/01/2016	54.7	N
98539	- 69.51	- 72.30	- 68.75	- 67.99	14/11/2015	30/12/2015	46.0	N
123006	- 69.52	- 72.31	- 72.01	- 76.69	14/11/2015	20/01/2016	66.8	Y
131004	- 69.52	- 72.34	- 70.43	- 80.22	16/11/2015	28/12/2015	41.7	N
131005	- 69.501	- 72.31	- 69.67	- 75.66	17/11/2015	22/12/2015	34.3	N
131429	- 69.25	- 69.82	- 68.83	- 67.97	18/11/2015	04/01/2016	46.3	N
131432	- 69.52	- 72.37	- 68.83	- 68.95	25/11/2015	10/01/2016	45.2	Y
131433	- 68.25	- 65.72	- 69.48	- 72.06	25/11/2015	20/01/2016	55.6	Y
150624	- 69.50	- 72.41	- 70.23	- 90.29	25/11/2015	06/01/2016	41.4	Y
150626	- 69.51	- 72.43	- 70.89	- 80.95	25/11/2015	09/12/2015	14.0	Y
150629	- 69.40	- 71.89	- 69.47	- 74.05	25/11/2015	18/01/2016	54.0	N
150630	- 69.51	- 72.33	- 68.91	- 68.59	25/11/2015	06/01/2016	41.9	N
150631	- 69.52	- 72.20	- 68.55	- 67.15	25/11/2015	05/01/2016	41.0	N
131430	- 69.51	- 72.29	- 70.01	- 77.39	18/11/2015	-	-	-

The onset of moult is gradual, before an individual stops foraging. One penguin, PTT_id= 131430 showed no evidence of slowing for moult

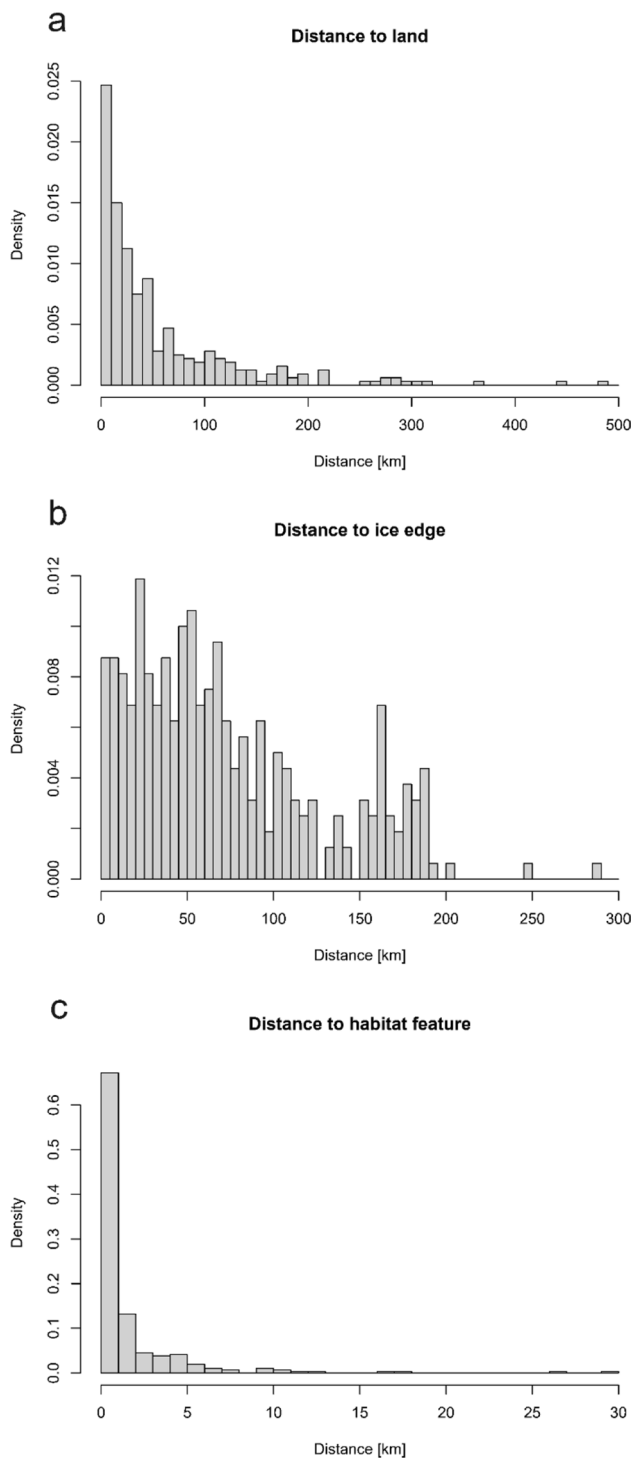


Fig. 4 Proximity to different features for each track point or cluster of points (mid-point of clusters) prior to moult: **a** coast line, **b** sea ice edge, and **c** open water feature (polynya, lead, iceberg > 120 m, or to land where tide cracks are postulated to occur)

et al. 2017; Emery et al. 1997). These devices moved on average at speeds of $\sim 0.8 \text{ km h}^{-1}$ (individual average speeds ranged from 0.1 to 1.8 km h^{-1}).

Habitat availability based on the historical satellite record

In almost all years, the PTT tracks recorded in November 2015 would have occurred within the historical sea ice extent, at least until 2020 (Fig. 7). However, in a few years, when sea ice was less extensive, a number of the November 2015 tracks would have fallen at least partially outside the historical sea ice extent.

Since 1979, there has been a decline in the average sea ice score (score 3, 2 or 1; full, partial or no sea ice, within the boxes identified in Fig. 6). In years when sea ice was partial, or not present, the penguins would have needed to find alternative moult locations requiring substantial relocation during some years (Fig. 8). In December, variability in sea ice extent was apparent from the late-1980s and early-1990s, whilst variability in January was apparent from the mid-1980s, and in February from the early-1980s. The level of variability was greatest in February, and least in December.

Discussion

Determining the preferred foraging habitats used by emperor penguins is important, given that their primary breeding and foraging habitats are projected to decline over the next decades (e.g. Jenouvrier et al. 2014, 2017, 2021). So far, most studies have focused upon changes in the breeding habitat (fast ice), but here we focus upon the preferred foraging and moulting habitat during summer; that is, the seasonal pack ice. We report the first telemetry data available to date for emperor penguins breeding at the west Antarctic Peninsula, a region that has been experiencing rapid, regional warming (Vaughan et al. 2001; Turner et al. 2016), glacial retreat (Cook et al. 2016), and rapidly decreasing sea ice extent and duration (Stammerjohn et al. 2012). The west Antarctic Peninsula is therefore a region that is likely to become increasingly unsuitable for supporting emperor penguins. The first emperor penguin breeding site assumed to have been lost in the current era occurs in this region (Trathan et al. 2011). Other colonies also exist along the west Antarctic Peninsula, including in the Bellingshausen Sea region. However, most of these are small, and many have only been recently discovered (Fretwell and Trathan 2020). It is unknown whether these small breeding sites were established following relocation from previous sites that were once favourable. Thus, the west Antarctic Peninsula presents an anthropogenically induced, large-scale experiment whereby parameters of emperor penguin populations and foraging patterns are being tested by the changing environment, providing an indication of what may happen elsewhere in the Antarctic as the planet warms, with the inevitable consequences projected by Jenouvrier et al. (2021).

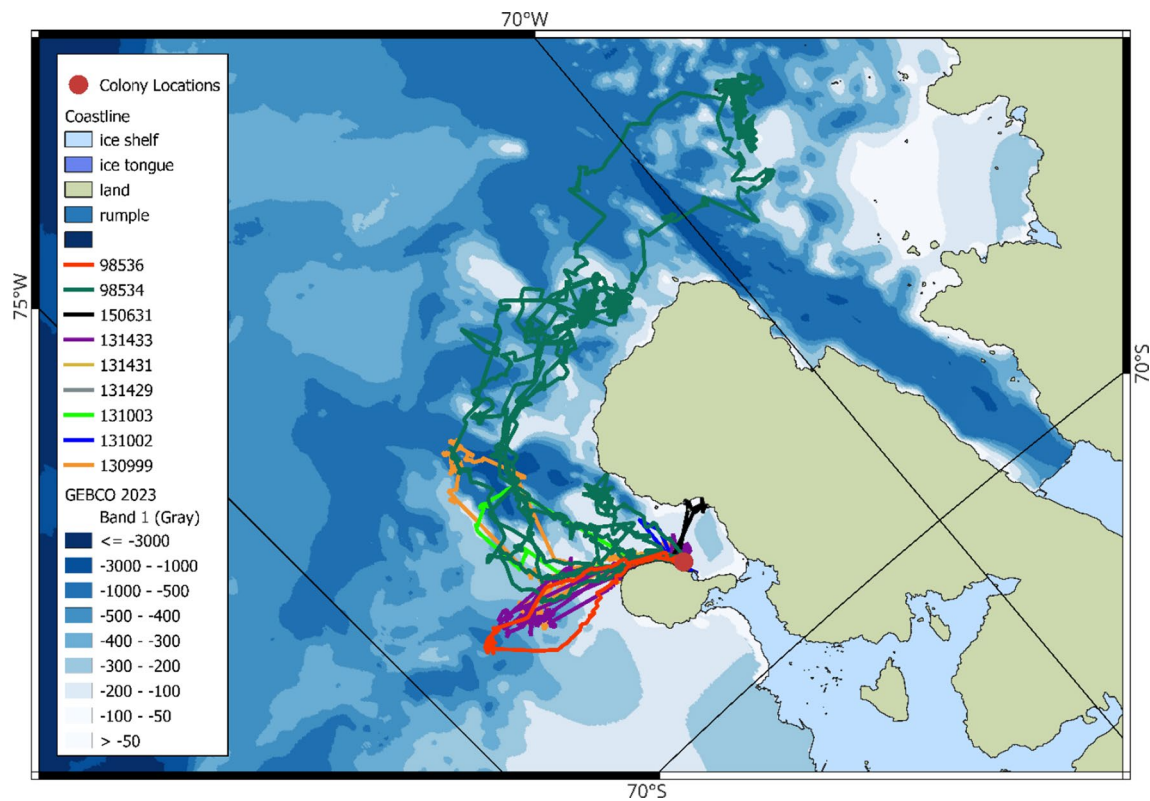


Fig. 5 Individual completed foraging trips of tracked adult emperor penguins that returned to the colony; see Table 1

Habitat use at the end of the breeding season in 2015/2016

During the 2015/2016 summer, sea ice extent reached an annual maximum of 18.8 million km² around 6 October 2015, coincident with the most extreme El Niño event since the early 1950s (climatedataguide.ucar.edu/climate-data/nino-sst-indices-nino-12-3-34-4-oni-and-tni; last accessed 01 August 2023). During 2015/2016, ice budget analyses have revealed that an east–west dipole of sea ice concentration anomalies was formed in autumn in response to El Niño-generated circulation changes (Pope et al. 2017). This dipole featured decreased ice concentration in the Ross Sea and increased concentration in the Amundsen and Bellingshausen seas (Pope et al. 2017). Thus, sea ice extent in 2015 remained above average off Wilkes Land, the Weddell Sea, and the Antarctic Peninsula (NASA 2015). By 18 October 2015, near to Rothschild Island, fast ice extended from the northern part of Marguerite Bay to the southern coast of Latady Island covering approximately 41,600 km². The distance from the Rothschild Island emperor penguin colony to the edge of the fast ice measured approximately 56 km. Leads of open water, about 5 to 6 km wide, were adjacent to the fast ice edge, but beyond was a ~200 km wide belt of pack ice. This contrasts with the situation in 2022 when a persistent

La Niña event was in process, associated with decreased sea ice extent (Wang et al. 2023; Simpkins 2023), and reported emperor penguin breeding failure at several colonies in the southern Bellingshausen Sea (Fretwell et al. 2023).

In our study, we were not able to identify breeding penguins, since we intercepted penguins *en route* to and from their colony. Given the timing of our study, we had anticipated that only a proportion of our tracked penguins would return to the colony from foraging trips. This proved to be the case; only nine of 33 penguins returned at least once post-deployment (Table 1; Fig. 5). However, other penguins that we fitted with ARGOS PTTs may also have been provisioning chicks, but because of early device failure (or attachment failure), we could not identify whether they were or not.

Based on the satellite tracks, those individual penguins still provisioning chicks utilised different areas in the wider neighbourhood of the colony. One penguin crossed the fast ice in Lazarev Bay and may have utilised tide cracks at the western coast of Alexander Island (Fig. 5), whilst others traversed the fast ice. These penguins hunted in the pack ice about 100 km to the west or north of Rothschild Island, whilst one individual foraged north of Alexander Island in southern Marguerite Bay where both pack ice and small areas of open water existed. All penguins remained within

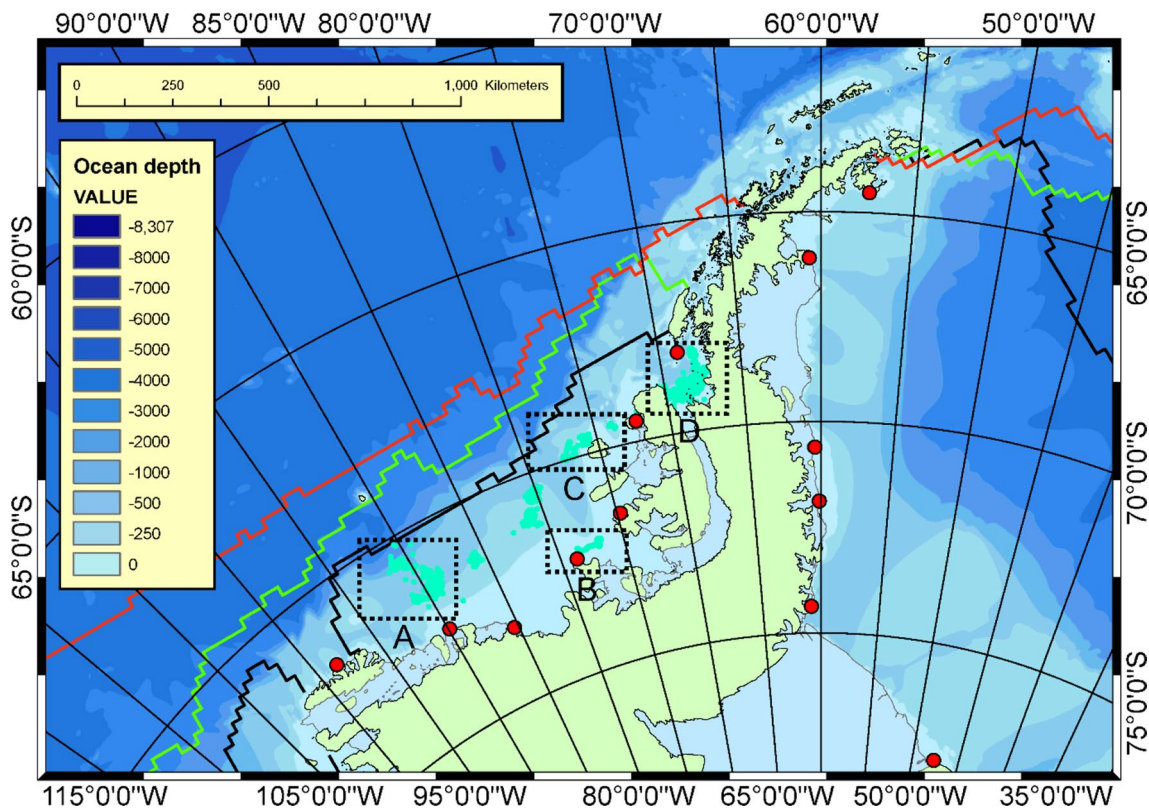
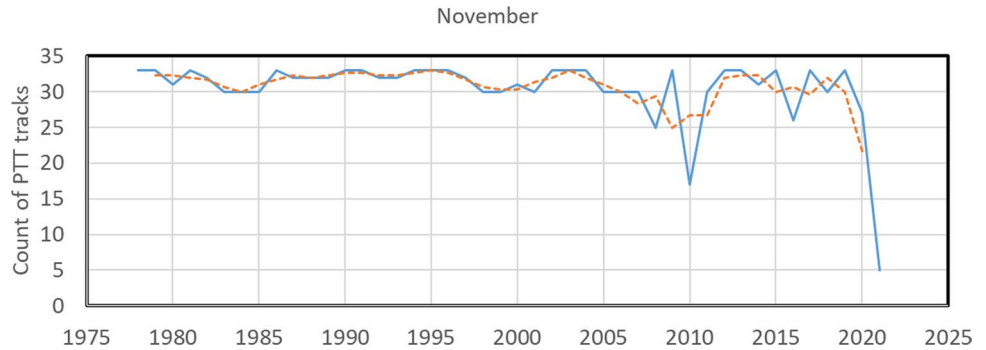


Fig. 6 Apparent stationary periods for 18 emperor penguins that were considered to have stopped travelling in anticipation of their annual moult, with times ranging from 9 December 2015 to 20 January 2016; see Table 2. Areas scored for inter-annual variation in monthly sea ice extent during December, January, and February are A—north

of Pflogner Point, B—north of Smyley Island, C—West of Charcot Island, and D—Marguerite Bay. Sea ice edge in December 2015 (red), January 2016 (Green), and February 2016 (Black) from NOAA dataset GO2135

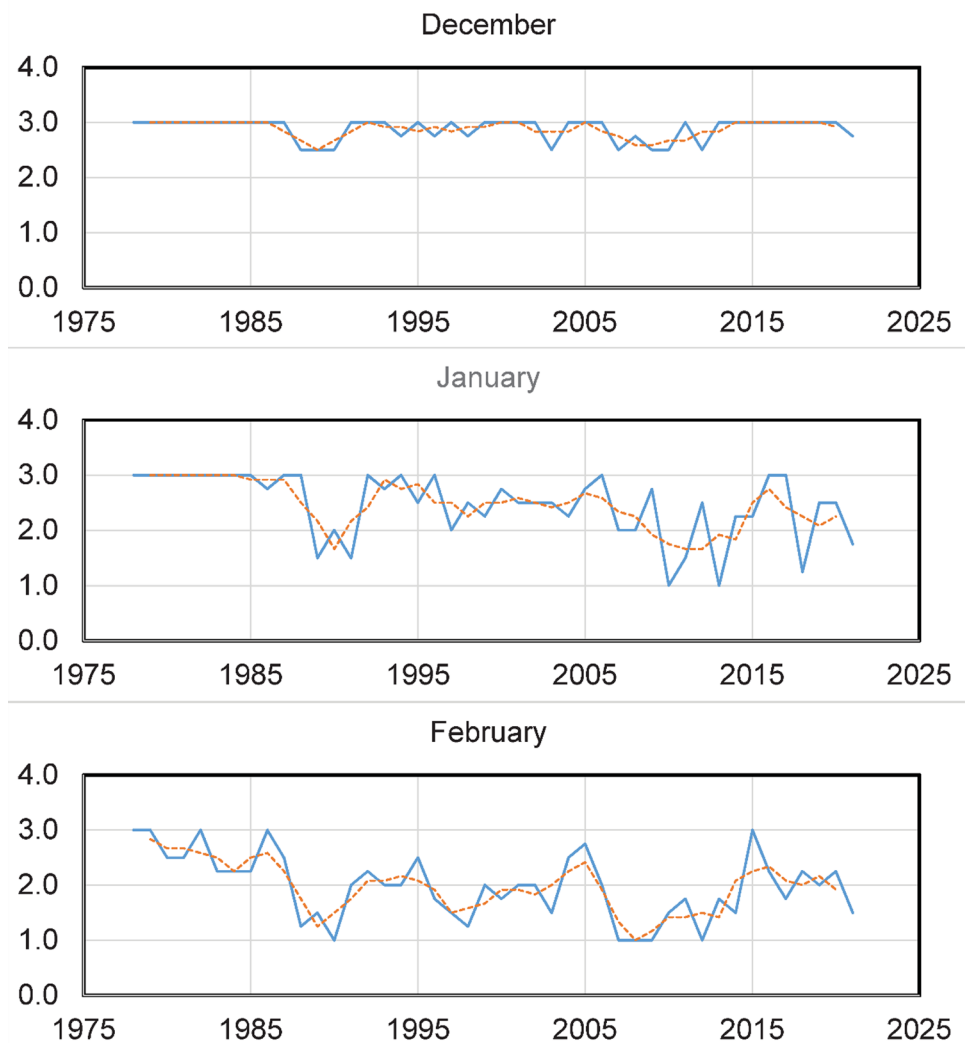
Fig. 7 Count of the number of foraging tracks from November 2015 that would have been completely within the seasonal sea ice in different years, assessed against the NOAA dataset GO2135 (see Methods): blue—track count; orange—3-year moving average



100 km of the coast (Fig. 4a), mostly well within the seasonal pack ice zone above the continental shelf (Fig. 4b) and close to habitat features that offer possible access to open water (Fig. 4c). Sea ice is a dynamic habitat, and though we found that almost half of the tracking centroids were close to leads within the sea ice, the location of these, and other habitat features, will likely change over time. Plausibly, over time, existing leads will move, some may close and other new ones may open, nevertheless leads are likely to remain a key feature for foraging emperor penguins.

This result supports the view that emperor penguins preferentially feed within the pack ice zone whilst still feeding their offspring (see Trathan et al. 2020). On average, return trips were short and ranged from ~4 to ~18 days (mean 9.6 ± 3.7 days), reaching a mean maximum distance from the colony of approximately 75 ± 45 km (range ~13–195 km). Individuals that performed more than one trip tended to return to the same area they had visited on previous trips. Thus, when foraging is successful in a certain area, it is worth returning.

Fig. 8 Sea ice scores (averaged across four locations: A—north of Pfrogner Point, B—north of Smyley Island, C—west of Charcot Island, and D—Marguerite Bay; see Fig. 6) showing inter-annual variation in monthly sea ice extent during moult (December, January, and February) from NOAA dataset GO2135 (see Methods): blue—sea ice score for full sea ice cover (score 3), partial sea ice cover (score 2), and no sea ice cover (score 1); orange—3-year moving average



Similar observations have previously been made elsewhere. For example, at Pointe Géologie, Adélie Land, chick-rearing emperor penguins undertook trips in spring (late October to mid-December 2005) that averaged 7 ± 1 days (range 2–19 days), with a mean maximum distance from the colony of 85 ± 8 km (range 21–163 km). These penguins also foraged mainly over the continental shelf (Zimmer et al. 2008). However, at Pointe Géologie, the shelf is relatively narrow and a proportion of foraging was over deep water (Zimmer et al. 2008). In contrast, at the much larger colonies of Coulman Island and Cape Washington, foraging is often over submarine banks of 400 m depth (Kooyman et al. 2020), and foraging is likely to include benthic or near benthic feeding. The GEBCO bathymetry that we used in our study (<https://www.gebco.net/>; accessed 13 March 2024) was of relatively coarse resolution both around Rothschild Island and in Marguerite Bay, with the available depth contours most likely imprecise close to land. However, foraging to the west of Rothschild Island and within Marguerite Bay

included activity over a series of banks where the bathymetry extended deeper than 500 m. This suggests that, as for the Ross Sea colonies, foraging was likely to be within the water column over areas of complex bathymetry (Kooyman et al. 2020).

Habitat use post-breeding and during moult in 2015/2016

In the life cycle of penguins, the annual moult is a crucial event as it can negatively affect adult survival and hence population dynamics, if unsuccessful. The moult is a complex and energy intensive physiological process. In contrast to flying birds that replace their feathers gradually over several months, penguins undergo a ‘catastrophic’ moult during which their entire plumage is replaced within a matter of weeks. Old feathers are pushed out by the emerging new ones, so the plumage is no longer waterproof. This also likely affects the streamlining of a penguin and probably

increases the energy an individual needs to expend when travelling (Wilson 1985). Since penguins have to acquire sufficient body reserves to moult successfully, this is potentially a problem. Emperor penguins have to balance their need to deposit adequate body reserves with their need to haul out because their plumage is no longer waterproof, as they could experience issues with their thermoregulation (Erasmus et al. 1981). Without visual confirmation, it is difficult to ascertain when exactly the moult process is sufficiently far advanced, that individuals must stop foraging, haul out, and fast, whilst moult proceeds.

To moult successfully, emperor penguins must first increase their body mass significantly from an average of 25 kg (cf SM Table 1; mean = 27.8 kg, range 24.5–33.0 kg) at the time of departure from the colony (Kooyman et al. 2000) to nearly 40 kg to withstand the weight loss they suffer during the moult (Kooyman et al. 2004). Thus, adults have to hunt extensively to prepare for the moult. Part of a successful moult strategy may also be a reduction in intraspecific competition for resources. To achieve this, they may travel longer distances and disperse over a larger area than during the chick-rearing period (Wienecke et al. 2004). Emperor penguins must also find a moult platform that remains stable for the duration of the moult (approximately 35 days, Gearhart et al. 2014). Although some adults return to their breeding colony to moult, many seek safety a long way from their breeding site, such as on fast ice, in dense pack ice, or even, where possible, on land, the continental ice sheet, or an ice shelf.

In 2015/16, 18 emperor penguins from Rothschild Island were tracked to their moult sites. The timing of moult varied; some penguins apparently initiated moult in early December and others as late as mid-January (Table 2). Moulting sites were some distance from the breeding site, ranging from about 230 km (Marguerite Bay) to > 800 km (north of Farwell Island (72° 51' S, 91° 05' W) and Pfrogner Point). None of the tracked birds returned to the breeding site. All moult areas were located in dense pack ice over the continental shelf (Fig. 6), but from December 2015 to February 2016, the pack ice became increasingly separated from the coast by open water (SM Fig. 1).

An indication that penguins have reached their moult site is a general slowing of their travel speed. Kooyman et al. (2000) reported that travel speeds prior to moult averaged 47.1 km day⁻¹ (equivalent to ~2.0 km h⁻¹). The speeds we observed during late chick rearing (1.7 km h⁻¹; Table 1) or prior to moult (~2.3 km h⁻¹) were therefore similar to those previously reported. Penguins are likely to be travelling at speeds that also allow intensive foraging *en route* to their moult sites. In comparison, once more advanced moult commenced, penguins in the Ross Sea moved on average 7.1 km day⁻¹ (0.3 km h⁻¹) (Kooyman et al. 2000), presumably either due to active movement or ice drift. At the Antarctic

Peninsula, during and subsequent to moult, emperor penguins moved at similar speeds (~0.8 km h⁻¹) to those tracked in the Ross Sea, albeit it somewhat faster. That may have been a consequence of more loose, faster drifting pack ice. Furthermore, variability in the quality and accuracy of PTT can lead to apparent movement; however, continuous ice drift over a number of days could lead to substantial directional displacement. For example, ice buoys drifted at speeds of 10.0 to 14.5 cm s⁻¹ (equivalent to 0.4–0.5 km h⁻¹) in the Amundsen Sea (Assmann et al. 2005), highlighting that moult sites are potentially quite mobile.

In 2015/2016, the sea ice extent along the west Antarctic Peninsula was extensive and completely encompassed the sites we identified as candidate moult sites. Even by February, the ice edge was only just beginning to recede towards the moult sites (Fig. 6).

Habitat availability based on the historical satellite record

Based on the extent and duration of sea ice in 2015/2016 (see Fig. 6 and SM Fig. 1), emperor penguins were unlikely to have been constrained in the habitat available to them during the late-breeding period, especially given the fact that sea ice was more extensive and lasted longer compared with the regional trend observed over the satellite era (Stammerjohn et al. 2012). Nevertheless, assuming that similar foraging conditions were also necessary in previous years, then it is likely that similar sea ice habitat would have been available during most years between 1979 and 2016, based on the satellite record (Fig. 7). Only in the most recent years has habitat quality declined towards the end of the breeding period (Fig. 7). Consequently, compared with November 2015, penguins may have had to relocate foraging effort (e.g. in 2021), or forage in open water particularly for longer-ranging foraging trips. Further, if preferred habitats are now more limited than previously, competitive effects may have increased.

In contrast, post-breeding habitat use would have become increasingly limited earlier in the satellite record, if the moult locations our study penguins selected in 2015/2016 are a reliable indicator of where penguins preferentially hauled out in other years (Fig. 8). For birds that begin moult early, completing moult by the end of December, ice conditions would probably have been satisfactory; however, for penguins extending moult into January or even February, the locations used in 2015/2016 would have been increasingly unreliable (Fig. 8). With the variation in sea ice extent observed over recent decades (Stammerjohn et al. 2012), regular monitoring of moult locations would increase understanding about how emperor penguins locate moulting platforms in years with different sea ice characteristics,

including whether individuals choose the same location, when suitable sea ice is present.

Such analyses provide an indication of plausible change, representative of increasing stress on emperor penguin populations breeding at the west Antarctic Peninsula, but at times of year not previously considered. Such changes will also plausibly happen in the future at other sites into the future as sea ice projections materialise (e.g. Jenouvrier et al. 2021). Nevertheless, with only a single year of telemetry data available, there are inevitably large uncertainties, necessitating a number of assumptions when assessing past and future habitat use and availability. Probably, the most important assumptions are that emperor penguins forage within the sea ice zone late in the breeding season and prior to moult (Trathan et al. 2020) and that the satellite archive provides a useful proxy of available habitat.

At present, serendipity and the logistical complexity of acquiring additional telemetry data from colonies at the west Antarctic Peninsula in years with extensive sea ice is unlikely. Any further work will depend upon the continuation or reversal of the current extremely low sea ice conditions. If such data can be acquired in the future, including from other regions where sea ice is also highly variable, then empirical comparisons between years with extensive sea ice and years with low or less extensive sea ice would reduce levels of uncertainty.

Of particular importance will be future investigations that help provide information about the physiological consequences of altered habitat, including on foraging and offspring provisioning, as well as the potential consequences of locating suitable platforms for moult. If sea ice habitats and sea ice-associated food webs change, provisioning rates will also change. Potentially, the energetic requirements required to find and locate stable moult platforms may also increase. Further, without a stable platform for moult, it is unclear how moult can proceed, something which is likely to be of critical concern.

Conclusion

The at-sea habitat available to emperor penguins when breeding is restricted. Colonies are located at approximately regular intervals around the Antarctic coastline, with a median separation distance of 324 km; mean 311, SD 176 km (Ancel et al. 2017). This suggests that penguins must find suitable prey within a radius of approximately 162 km. This is similar to the maximum furthest distance travelled from the colony (195 km) in our study (Table 1; mean 75 ± 45 km). The distance travelled is plausibly also related to the average travel speeds of adults and the average periods between feeds that chicks can sustain when both parents are provisioning. Thus, the resources within a relatively limited

sea scape must support the combined demands of both parents and indeed the whole colony.

Offspring provisioning success may be compromised, should emperor penguin preferred sea ice habitats change, either between years, or over time, especially if such changes also lead to differences in available prey composition and abundance (cf Constable et al. 2014) within the accessible sea scape. Certainly, based on the major changes observed in sea ice habitat along the west Antarctic Peninsula within recent years, it is unsurprising that the west Antarctic Peninsula is now hostile for chick-rearing emperor penguins. Only small colonies exist and one is now probably functionally extinct (Trathan et al. 2011).

After breeding, adults are less constrained as they no longer need to provision their offspring. Therefore, preferred adult moult locations may not be regularly separated (cf Ancel et al. 2017). Nevertheless, it might be anticipated that pre-moult foraging locations are close to the eventual moult location, if penguins attempt to minimise energy expenditure in anticipation of the high energetic demands of moult. Therefore, again based on the changes in sea ice habitat in recent years, moult locations may now be very widely distributed and remote from the colony as they are for the Ross Sea. It is important to note that Kooyman and Mastro, (2023) consider that moult is the most dangerous phase of activity for adult emperor penguins.

Developing an improved understanding about foraging success and moult success in areas where sea ice varies inter-annually would help improve projections of how emperor penguin population parameters may change as global warming continues. The Antarctic Peninsula offers unprecedented insights into the future, as in this area over the period 1979/1980 to 2010/2011, seasonal sea ice advance has been $+1.9 \pm 0.5$ days later per year, seasonal sea ice retreat has been -1.2 ± 0.4 earlier per year, and sea ice duration has been -3.1 ± 1.0 days shorter per year (Stammerjohn et al. 2012).

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Author contributions PNT and BW acquired project resources, planned, and undertook all fieldwork. PNT, AF, and LI undertook analyses. PNT and BW developed the figures. PNT and BW wrote the first draft and all authors reviewed the manuscript.

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Data availability The ARGOS telemetry data used in this study are available from the UK Polar Data Centre (<https://www.bas.ac.uk/data/uk-pdc/>).

Declarations

Competing interests The authors have no competing interests to declare that are relevant to this work.

Ethical approval The joint Cambridge University/British Antarctic Survey Animal Ethics Committee and the Australian Antarctic Division Animal Ethics Committee approved all animal handling procedures used in this study. We declare that all applicable guidelines for the care of wildlife in this study were followed.

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