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Breeding emperor penguins show interannual recurrence in shelf-break associated foraging areas across contrasting sea ice conditions in the northwestern Weddell Sea

Hugo R. Guímaro[1,2,3]✉, Peter T. Fretwell[3], Klemens Pütz[4], José C. Xavier[1,2,3], Victoria Warwick-Evans[3], George Day[3], Juliana A. Vianna[5,6,7], Eduardo J. Pizarro[6,7,8], Lucas Krüger[7,9], Neil E. Osborne[10] & Norman Ratcliffe[3]

The emperor penguin *Aptenodytes forsteri* is highly sea ice dependent and vulnerable to climate change, yet the at-sea distribution and habitat associations of breeding adults remain poorly understood for colonies in the western Weddell Sea. We tracked nine breeding adults from Snow Hill Island, the northernmost known colony, during chick-rearing in 2023-24 and 2025-26, and analysed 38 foraging trips using kernel utilisation distributions, habitat-selection models and hidden Markov models. Penguins repeatedly used a region east and northeast of the colony aligned with shelf-break-associated waters, with a smaller westward component towards waters close to glaciated coastal margins along the Antarctic Peninsula. Space use was broader and trips were longer in 2025-26, when core-use areas occurred under much higher sea ice concentration, yet overlap metrics indicated broad fidelity to the same geographical foraging region. Habitat use was associated with distance to the colony, mean sea ice concentration, with responses differing between study years, and the combined influence of shelf-break position and distance to glaciated coastal margins. Behavioural states varied with diel cycle and sea ice concentration, with foraging and resting associated with higher sea ice concentration than transit. The proposed Weddell Sea Marine Protected Area encompassed 57.9–75.1% of study-year foraging distributions, while smaller overlap occurred with the proposed Western Antarctic Peninsula and South Scotia Arc Marine Protected Area, highlighting the relevance of these areas for spatial conservation planning.

Keywords *Aptenodytes forsteri*, Satellite tracking, Habitat selection, Sea ice, Weddell Sea, Marine protected areas

Understanding where marine predators forage, which habitat preferences underpin their distributions, and whether individuals or populations repeatedly use particular areas is fundamental for evaluating their ecological requirements and conservation needs[1,2]. This is particularly important in regions vulnerable to rapid

[1]Associate Laboratory TERRA, Department of Life Sciences, Centre for Functional Ecology – Science for People and the Planet (CFE), University of Coimbra, Calçada Martim de Freitas, 3000-456 Coimbra, Portugal. [2]Associate Laboratory TERRA, Centre for Functional Ecology – Science for People and the Planet (CFE), University of Coimbra Campus at Figueira da Foz, Quinta das Olaias, 3080-183 Figueira da Foz, Portugal. [3]British Antarctic Survey, Natural Environment Research Council, Cambridge CB3 0ET, UK. [4]Antarctic Research Trust, Bremervörde, Germany. [5]One Health Institute, Faculty of Life Sciences, Universidad Andrés Bello, Santiago, Chile. [6]Millennium Institute Center for Genome Regulation (CGR), Santiago, Chile. [7]Millennium Institute Biodiversity of Antarctic and Subantarctic Ecosystems (BASE), Santiago, Chile. [8]Facultad de Ciencias Biológicas, Pontificia Universidad Católica de Chile, Santiago, Chile. [9]Departamento Científico, Instituto Antártico Chileno INACH, Punta Arenas, Chile. [10]School of the Environment, Trent University, Peterborough, ON, Canada. ✉email: guimaro.hugo@gmail.com

environmental change, such as the polar regions[3,4]. The emperor penguin *Aptenodytes forsteri* is a strongly sea ice-dependent predator, relying on stable fast ice as a breeding platform and on sea ice-associated habitats for foraging and resting during chick-rearing and moulting[5–9]. It is considered one of the most vulnerable species in Antarctica to climate change[10–14] and was recently reclassified from "Near Threatened" to "Endangered" on the IUCN Red List due to projected population declines in response to climate-driven loss of sea ice habitat[15]. However, despite its ecological and conservation relevance as a sea ice dependent predator, the emperor penguin is not yet considered a specially protected species under the Antarctic Treaty[14]. Despite recent advances in satellite-based colony monitoring and targeted telemetry, detailed knowledge of emperor penguin at-sea distribution, foraging areas, and habitat associations remains limited, largely because many colonies are remote and logistically challenging to access[16,17].

Recent years have seen substantial environmental shifts across the Southern Ocean, including abrupt reductions in Antarctic sea ice extent[4,18]. These changes are particularly relevant along the Antarctic Peninsula and adjacent regions, where reductions in sea ice duration and broader climate-driven ecosystem changes have been well documented[19–21]. Emperor penguins are particularly sensitive to such changes because stable fast ice provides the breeding platform, while sea ice conditions also influence prey availability and the energetic costs of foraging throughout their annual cycle[7,22–24]. For example, in 2022, record-low sea ice extent led to the first observation of regional level early breakup of sea ice at breeding colonies in the Bellingshausen Sea, which was likely the main cause of the massive breeding failures observed that year[25].

During chick-rearing, emperor penguins must balance foraging, travelling and resting at sea with frequent returns to the colony to provision chicks, linking both their use of space and allocation of time to chick growth, survival and future recruitment[2,26–28]. These behavioural patterns may also vary with environmental and diel conditions. At sea, emperor penguins typically exploit polynyas, leads and pack ice zones, which can facilitate access to abundant prey resources[17,28]. However, the use of these areas remains poorly documented, particularly for colonies located in more northerly and potentially vulnerable regions, where interannual sea ice variability may influence prey distribution and foraging behaviour[29,30]. Identifying consistently utilised foraging areas and the habitat features associated with their use is therefore important for understanding breeding-season ecology and informing spatial conservation planning[17,31].

The Weddell Sea region is a major stronghold for emperor penguins: although it contains approximately 14 colonies, representing 20% of all known colonies, these colonies support approximately one-third (~ 33%) of the global emperor penguin population[16]. Located in the northern Weddell Sea, Snow Hill Island (Fig. 1) hosts the northernmost known emperor penguin colony and lies close to the eastern Antarctic Peninsula margin, where sea ice conditions are shaped by regional circulation and by seasonal and interannual variability in the position of the marginal ice zone. Despite the importance of the Weddell Sea region and the unique geographical position of Snow Hill Island, no tracking studies have yet been published from emperor penguin colonies in the western Weddell Sea sector. Given the ongoing changes in Antarctic sea ice extent and duration[32,33], and in landfast ice area[34], understanding how emperor penguins at the northern limit of the species' breeding distribution use, and repeatedly return to, particular foraging areas is increasingly important for informing spatial conservation planning in the Weddell Sea, including by assessing their overlap with proposed marine protected areas in the Weddell Sea and adjacent Antarctic Peninsula region.

Our study uses satellite tracking, habitat-selection models and hidden Markov models to investigate chick-rearing space use, habitat associations and behavioural states of breeding emperor penguins at Snow Hill Island across two study years (2023-24 and 2025-26). Specifically, we aimed to (1) identify recurrent foraging areas and core-use areas used during chick-rearing; (2) test whether habitat use was associated with distance from the colony, position relative to the continental shelf-break, sea ice concentration, and distance to glaciated coastal margins; (3) measure how resting, transit and foraging states varied spatially and with sea ice and diel conditions; and (4) evaluate the spatial overlap between recurrent foraging areas and the proposed Weddell Sea Marine Protected Area and Western Antarctic Peninsula and South Scotia Arc Marine Protected Area. By linking space use, habitat associations and behaviour, our study provides new insight into how breeding emperor penguins use foraging areas under variable sea ice conditions and provides spatially explicit information relevant to conservation planning in the northwestern Weddell Sea.

Results

Tracking overview and foraging trip characteristics

The dataset comprised 38 complete foraging trips from nine breeding emperor penguins collected during chick-rearing: 23 trips from four individuals in 2023-24 and 15 trips from five individuals in 2025-26 (Table S1). Breeders completed between five and six trips each in 2023-24 and one to six trips each in 2025-26. Following return from foraging trips, inferred breeders spent short periods at the colony before departing again, likely associated with chick provisioning and parental attendance, averaging 1.8 ± 0.4 days in 2023-24 and 1.8 ± 0.7 days in 2025-26. Trip duration was longer in 2025-26 than in 2023-24, increasing from 4.8 ± 2.5 days to 10.5 ± 9.3 days. Although the unadjusted linear mixed model indicated a study-year effect ($F_{1,36}$ = 4.29, p = 0.046), this was not retained after correction (adjusted p = 0.182; Table 1). None of the other trip metrics showed statistical support for differences between study years after adjustment. Total trip distance and maximum distance from the colony were also highly variable within study years. The longest trip recorded in 2025-26 lasted 34 days, covered 2,079.8 km, and reached 478.4 km from the colony (Table S1).

Tracks from both study years were directed predominantly east and northeast of Snow Hill Island, towards the shelf-break sector of the northwestern Weddell Sea (Fig. 1). A smaller west to west-northwest component towards waters close to glaciated coastal margins along the eastern Antarctic Peninsula coast was also evident but was driven by a limited number of individuals: one individual in 2023-24 used this western coastal sector across all its trips, while in 2025-26 one individual made repeated trips towards this coastal sector after an initial longer

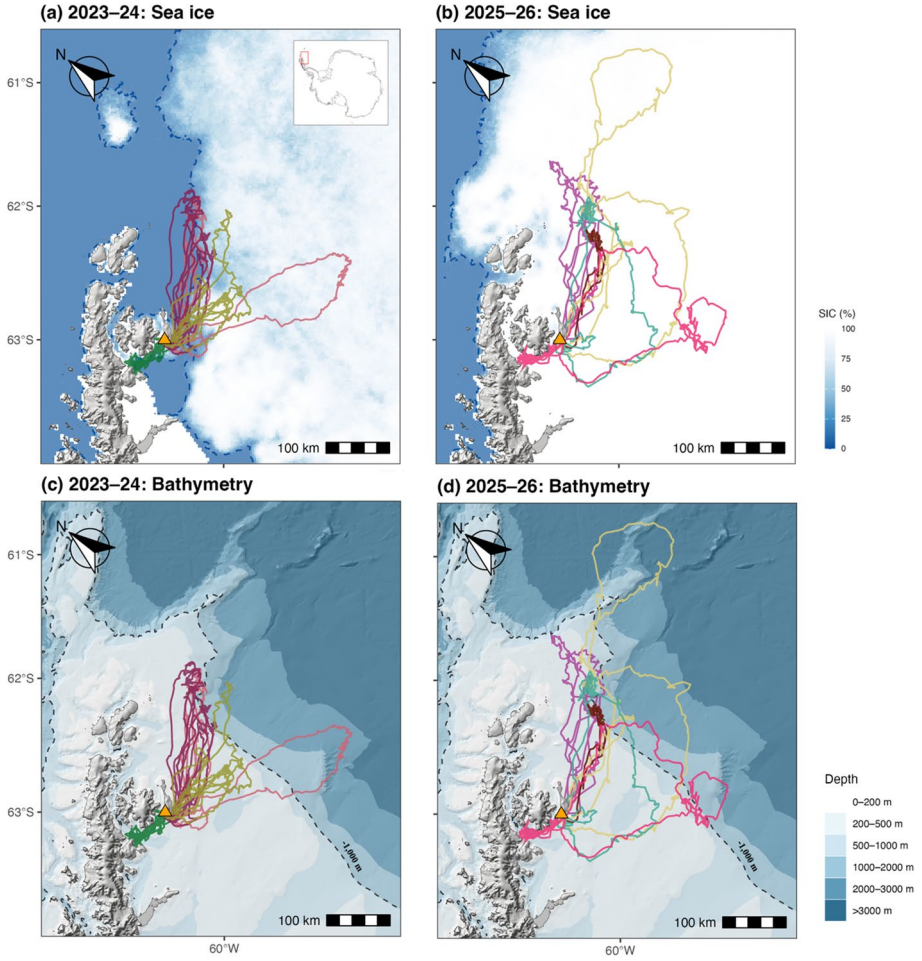


Fig. 1. Chick-rearing tracking paths of breeding emperor penguins from Snow Hill Island during the 2023-24 and 2025-26 study years in relation to sea ice and bathymetric conditions. Top panels (**a**, **b**) show individual tracks over December median sea ice concentration, with the 5% sea ice concentration contour representing the outer low-concentration ice margin; bottom panels (**c**, **d**) show the same tracks over hillshaded bathymetry, with the dashed black contour indicating the − 1,000 m isobath, used here as a proxy for the continental shelf break. Coloured lines distinguish individual breeder tracking paths, and the orange triangle marks the colony location.

offshore trip. An additional 2025-26 individual also moved in the same general direction before transmission ended and the trip was excluded from formal analyses. In 2025-26, tracks from three individuals appeared to be spatially associated with the large iceberg southwest of the colony, with some movements extending farther south and offshore than those recorded in 2023-24 (Fig. S1).

Interannual space use and overlap

Study-year kernel UDs showed recurrent use of a geographical foraging region east and northeast of Snow Hill Island during chick-rearing, with a smaller but consistent westward component towards waters close to glaciated coastal margins along the eastern Antarctic Peninsula. Space use was broader in 2025-26 than in 2023-24 (Fig. 2). The 50% UD, representing the core-use area, covered 12,511.2 km^2 in 2023-24 and 13,218.7 km^2 in 2025-26, while the 95% UD covered 51,016.5 km^2 and 83,776.4 km^2, respectively (Table 2). Overlap metrics indicated broad spatial similarity between study years, although core-use areas were not identical. Bhattacharyya's affinity between the full utilisation distributions was 0.822. Overlap in utilisation intensity was higher across the 95% UDs than within the 50% UDs, with UDOI values of 0.865 and 0.126, respectively. Overall, these results indicate that breeders used a similar east-northeastern region in both study years, while the distribution of core use differed within that broader region in 2025-26.

Environmental summaries of the study-year UDs indicated that core-use areas in both years were predominantly associated with shelf and upper-slope waters, although deeper waters contributed more to the 2025-26 core area. In contrast, sea ice conditions differed between study years, with the 2025-26 UDs associated with substantially denser pack ice than those in 2023-24 (Table 2).

Panel A: Descriptive trip metrics						
Study year	**PTT ID**	**N trips**	**Trip duration (days)**	**Trip distance (km)**	**Furthest distance (km)**	**Inter-trip colony attendance (days)**
2023-24	237,206	5	5.7 ± 4 (2.7–12.0)	506.6 ± 293.2 (157.8–918.6)	198.0 ± 93.2 (68.3–319.9)	2.2 ± 0.6 (1.8–3.0)
	237,208	6	3.8 ± 1.6 (0.9–5.6)	213.9 ± 92.8 (41.3–295.7)	65.0 ± 14.9 (35.8–74.8)	1.7 ± 0.3 (1.3–2.2)
	237,680	6	4.8 ± 2.0 (2.0–7.9)	471.4 ± 186.9 (176.6–732.4)	179.0 ± 63.1 (68.3–239.3)	1.8 ± 0.1 (1.7–1.9)
	237,682	6	5.0 ± 2.6 (2.3–9.8)	374.0 ± 186.7 (164.8–719.9)	131.4 ± 53.1 (67.2–225.9)	1.7 ± 0.5 (1.4–2.6)
Mean ± SD	–	**5.8 ± 0.5**	**4.8 ± 2.5 (0.9–12.0)**	**386.5 ± 216.5 (41.3–918.6)**	**141.0 ± 76.9 (35.8–319.9)**	**1.8 ± 0.4 (1.3–3)**
2025-26	36,293	4	10.9 ± 6.7 (1.2–16.4)	588.7 ± 362.9 (53.0–826.4)	202.5 ± 106.4 (47.3–280.6)	2.0 ± 0.2 (1.7–2.1)
	43,642	1	10.1 ± 0.0 (10.1–10.1)	626.8 ± 0 (626.8–626.8)	180.7 ± 0.0 (180.7–180.7)	–
	43,643	2	21.6 ± 17.5 (9.2–34.0)	1,298.3 ± 1,105.2 (516.8–2,079.8)	335.2 ± 202.6 (192–478.4)	2.0 ± 0 (2.0–2.0)
	43,644	2	12.2 ± 13.1 (3.0–21.4)	788.0 ± 936.2 (126.0–1,450.0)	142.3 ± 122.5 (55.7–228.9)	3.5 ± 0 (3.5–3.5)
	43,648	6	6.0 ± 6.7 (2.5–19.6)	379.7 ± 471.8 (149.9–1,340.8)	102.9 ± 80.3 (60.1–266.2)	1.3 ± 0.3 (1.1–1.6)
Mean ± SD	–	**3.0 ± 2.0**	**10.5 ± 9.3 (1.2–34.0)**	**628.8 ± 593.6 (53.0–2,079.8)**	**170.9 ± 122.4 (47.3–478.4)**	**1.8 ± 0.7 (1.1–3.5)**
Percentage change	–	− 47.8%	+ 119.2%	+ 62.7%	+ 21.2%	− 1.4%

Panel B: Mixed-model comparisons					
	β **± SE**	**95% CI**	**F (df)**	**p**	**p adjusted**
Trip duration	0.51 ± 0.25	0.011–1.017	4.29 (1, 36.0)	0.046	0.182
Trip distance	0.24 ± 0.32	-0.537–1.018	0.55 (1, 6.5)	0.483	1.000
Furthest distance	0.18 ± 0.33	-0.593–0.958	0.31 (1, 7.1)	0.596	1.000
Inter-trip colony attendance	0.08 ± 0.20	-0.423–0.586	0.17 (1, 5.0)	0.694	1.000

Table 1. Summary statistics of all completed at-sea trips ($N = 38$) of tracked breeder emperor penguins during the chick-rearing periods of 2023-24 ($N = 23$ trips) and 2025-26 ($N = 15$ trips) at Snow Hill Island (Weddell Sea, Antarctica). Values are presented at both the individual and study-year levels as mean ± standard deviation (range). Study-year means were calculated from all completed trips undertaken by breeding individuals in each study year, and percentage change was calculated from study-year mean values for 2025-26 relative to 2023-24. Statistical differences between study years were assessed using linear mixed-effects models with study year as a fixed effect and individual as a random intercept. P-values were adjusted across the four metrics using the Holm method.

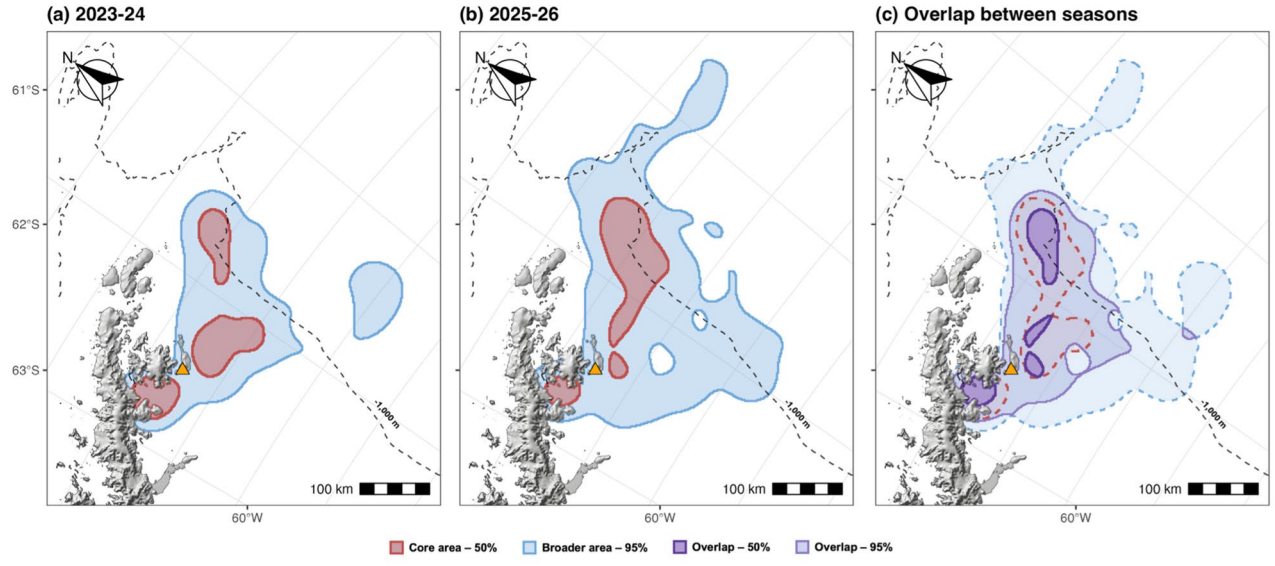


Fig. 2. Kernel utilisation distributions (UDs) summarising chick-rearing space use of breeding emperor penguins from Snow Hill Island during the 2023-24 and 2025-26 study years. Panels (**a**) and (**b**) show the study-year 50% UD, representing core-use areas, in red, and the 95% UD, representing broader-use areas, in blue. Panel (**c**) summarises the spatial overlap between study years, showing overlap of the 95% UDs in light purple and overlap of the 50% UDs in dark purple. The orange triangle marks the Snow Hill Island colony, and black dashed and dot-dashed contours indicate the − 1,000 m isobath, used here as a proxy for the continental shelf-break.

Study year	UD	Area (km²)	Depth (m)			Sea ice concentration (%)			Overlap (%)			
			Mean ± SD	Min - Max	Median	Mean ± SD	Min - Max	Median	CCAMLR Domain		WSMPA	D1MPA
									1	3		
2023-24	50	12,511.2	485.9 ± 243.2	11.6–1,593.1	420.3	42.3 ± 20.0	5.1–95.9	40.7	15.1	75.8	71.3	7.4
	95	51,016.5	911.2 ± 871.9	3.3–3,077.9	458.3	46.6 ± 28.7	0.1–96.4	49.4	13.1	79.5	75.1	6.6
2025-26	50	13,218.7	688.1 ± 496.1	13.9–2,152.5	435.5	97.0 ± 2.5	81.6–99.9	97.4	31.7	65.5	57.9	15.4
	95	83,776.4	955.9 ± 844.0	3.3–3,456.7	484.5	97.4 ± 4.1	42.2–100	98.6	27.2	67.9	64.9	7.1

Table 2. Summary of core and extended study-year foraging areas and their overlap with conservation/planning boundaries for tracked breeding emperor penguins from Snow Hill Island during the chick-rearing periods of 2023-24 and 2025-26. Core and extended foraging areas are represented by 50% and 95% kernel utilisation distributions (UDs), respectively. Area is reported in km², depth values in metres, and sea ice concentration in %. Depth and sea ice concentration values are summarised as mean ± SD, minimum - maximum, and median across raster cells within each UD polygon. Overlap with the proposed Weddell Sea Marine Protected Area (WSMPA) and the proposed Western Antarctic Peninsula and South Scotia Arc Marine Protected Area (Domain 1 MPA) is also quantified. Sea ice concentration values represent the distribution of mean SIC across the chick-rearing period within raster cells contained in each 50% and 95% UD. Interannual UD overlap was BA = 0.822; UDOI = 0.126 for the 50% UDs and 0.865 for the 95% UDs.

Habitat selection

Habitat selection during the chick-rearing period was best explained by a model including study year, distance from the colony, mean sea ice concentration (SIC), and a tensor interaction between signed distance to the 1,000 m isobath and distance to the glaciated coastal margin, with individual and trip included as random effects. The relationship between mean SIC and habitat use was allowed to vary between study years. The selected model explained 69.6% of deviance and received substantially greater support than models in which shelf-break position and distance to the glaciated coastal margin were included as additive effects (Table S2). Spatial predictions showed that areas of high relative probability of use were concentrated mainly east and northeast of Snow Hill Island, although the spatial extent of predicted high-use habitat differed between study years (Fig. 3).

Relative probability of use was highest within approximately 200–250 km of the colony and declined beyond this range (Fig. 4a). Mean SIC showed different responses between study years: in 2023-24, relative probability of use was highest at intermediate mean SIC of approximately 15–60%, whereas in 2025-26 it increased only at very high mean SIC corresponding to dense pack ice (Fig. 4b). Locations remained closely associated with sea ice in both study years. In 2023-24, 22.0% of locations occurred beyond the 5% SIC contour representing the outer low-concentration ice margin, but these were at most 39.2 km beyond this contour. In 2025-26, locations occurred almost entirely within this margin, with only 0.05% beyond the 5% SIC contour and at most 4.5 km from it. Modelled responses to shelf-break position and distance to the glaciated coastal margin showed higher predicted use in shallower shelf waters closer to glaciated coastal margins and in more offshore, shelf-break associated waters (Fig. 4c, d).

The population-level habitat model also showed strong predictive performance when individuals were excluded sequentially from model fitting. Leave-one-bird-out cross-validation produced a mean AUC of 0.947 ± 0.036, with mean sensitivity of 0.944 ± 0.082 and specificity of 0.866 ± 0.072. The selected tensor structure was also retained when tracking locations were progressively thinned to 6, 12 and 24 h intervals; at 24 h resolution, the tensor model remained supported than the corresponding additive model (ΔAIC = 2.19; Table S4). These sensitivity analyses indicated that the main habitat-selection pattern was robust to individual-level variation and reduced temporal sampling.

Behavioural states

The best-supported HMM transition model included additive effects of local solar time and sea ice concentration on state transition probabilities (Table S5). This model was better supported than models which included the interaction between local time and sea ice concentration (ΔAIC = 8.63), while models including only diel cycle or sea ice concentration had substantially lower support (ΔAIC = 54.61 and 131.99, respectively).

The decoded states and wet/dry patterns were consistent with behaviours interpreted as resting, foraging and transit. Resting was characterised by short movements, a low proportion of time immersed and weak directional persistence (mean step length = 1.77 km h^{-1}; mean ω = 0.11; wrapped-Cauchy concentration = 0.47). Foraging showed intermediate step lengths, a high wet proportion and intermediate directional persistence (2.24 km h^{-1}; ω = 0.72; wrapped-Cauchy concentration = 0.60), whereas transit was characterised by the longest movements, a high wet proportion and strong directional persistence (5.27 km h^{-1}; ω = 0.78; wrapped-Cauchy concentration = 0.84).

Based on the decoded state sequence, emperor penguins spent 37.2% of their at-sea time resting, 35.3% foraging and 27.5% transiting. When decoded at-sea behavioural states were combined with post-trip colony-attendance intervals, individuals spent most of the observed chick-rearing trip cycle at sea. Duration-weighted study-year time budgets indicated that at-sea time accounted for 72.5% of the observed trip cycle in 2023-24 and 86.9% in 2025-26, with the remaining 27.5% and 13.1% spent attending the colony, respectively (Table S6; Fig. S2). Across both study years, the full observed trip-cycle budget comprised 30.3% resting at sea, 29.4% foraging

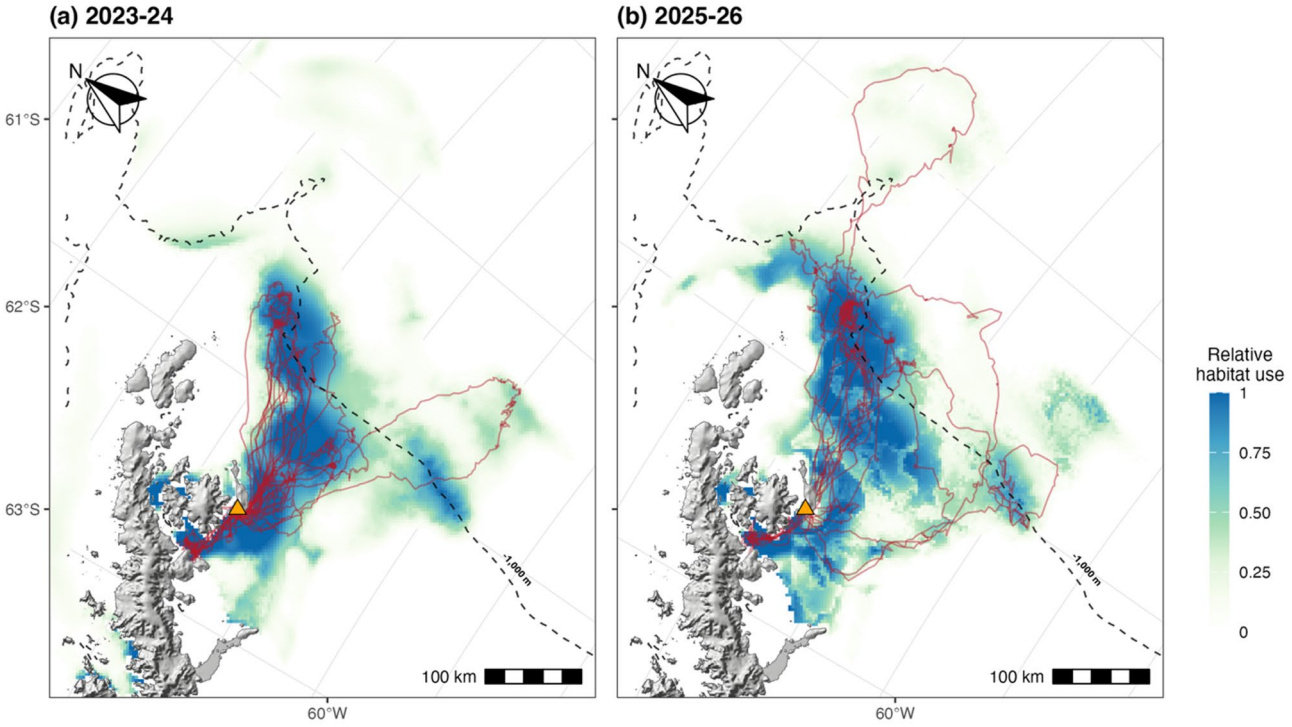


Fig. 3. Model-predicted relative habitat use of breeding emperor penguins from Snow Hill Island during chick-rearing. Panels show predicted relative habitat use during the (**a**) 2023-24 and (**b**) 2025-26 study years, derived from the final habitat-selection GAM. The model included a shared smooth effect of distance to the colony, study-year specific smooth effects of mean sea ice concentration, and a tensor interaction between signed distance to the 1,000 m isobath and distance to glaciated coastal margins, with bird and trip included as random effects. Predictions represent the population-level environmental component of the model, excluding bird and trip specific random effects. Red lines indicate the observed tracking paths, the dashed black line indicates the − 1,000 m isobath, used as a proxy for the continental shelf-break, and the orange triangle marks the colony.

at sea, 20.7% transiting at sea and 19.6% attending the colony. The decoded behavioural states also showed spatial structure across trips, with transit states generally associated with directional outbound and inbound movements (Fig. 5a–c).

Behavioural states also varied over the diel cycle (Fig. 5d). Resting was most common during the early morning, peaking between 03:00 and 05:00 local time, when it represented approximately 64–66% of decoded states. Transit was most frequent around midday, representing approximately 36–37% of decoded states between 10:00 and 12:00. Lastly, foraging increased later in the day and was highest during the evening, reaching approximately 47–49% of decoded states between 19:00 and 21:00.

Foraging and resting occurred in areas with higher mean sea ice concentration than transit, with values of 84%, 80% and 62%, respectively. Moreover, in 2023-24, 13% of foraging-state locations occurred beyond the 5% SIC contour representing the outer low-concentration ice margin, compared with 16% of resting and 38% of transit locations. In contrast, decoded locations in 2025-26 occurred almost entirely within dense pack ice, with 99.5% of foraging, 99.8% of resting and 98.1% of transit locations. Foraging-state locations occurred over slightly deeper seafloor than resting and transit locations, with mean seafloor depths of 874 m, 767 m and 715 m, respectively.

Foraging areas relative to conservation-planning boundaries

The at-sea distribution of emperor penguins overlapped CCAMLR Planning Domain 1 "Western Antarctic Peninsula-South Scotia Arc" and Domain 3 "Weddell Sea", as well as the proposed Weddell Sea Marine Protected Area (WSMPA) and the proposed Western Antarctic Peninsula and South Scotia Arc Marine Protected Area (Domain 1 MPA) (Fig. 6). Across study years and UD levels, most of the utilisation distributions occurred within CCAMLR Planning Domains 1 and 3, with the greatest overlap consistently occurring in Domain 3. Overlap with the proposed WSMPA was considerable but varied between study years and UD levels. In 2023-24, 71.3% of the 50% UD and 75.1% of the 95% UD overlapped the proposed WSMPA, compared with 57.9% and 64.9%, respectively, in 2025-26. Where study-year UDs overlapped the proposed WSMPA, overlap occurred within the mapped General Protection Zone. Overlap with the proposed D1MPA was smaller, accounting for 7.4% and 6.6% of the 50% and 95% UDs in 2023-24 and 15.4% and 7.1% in 2025-26, respectively (Table 2). However, parts of the chick-rearing distribution extended beyond the boundaries of both proposed MPAs.

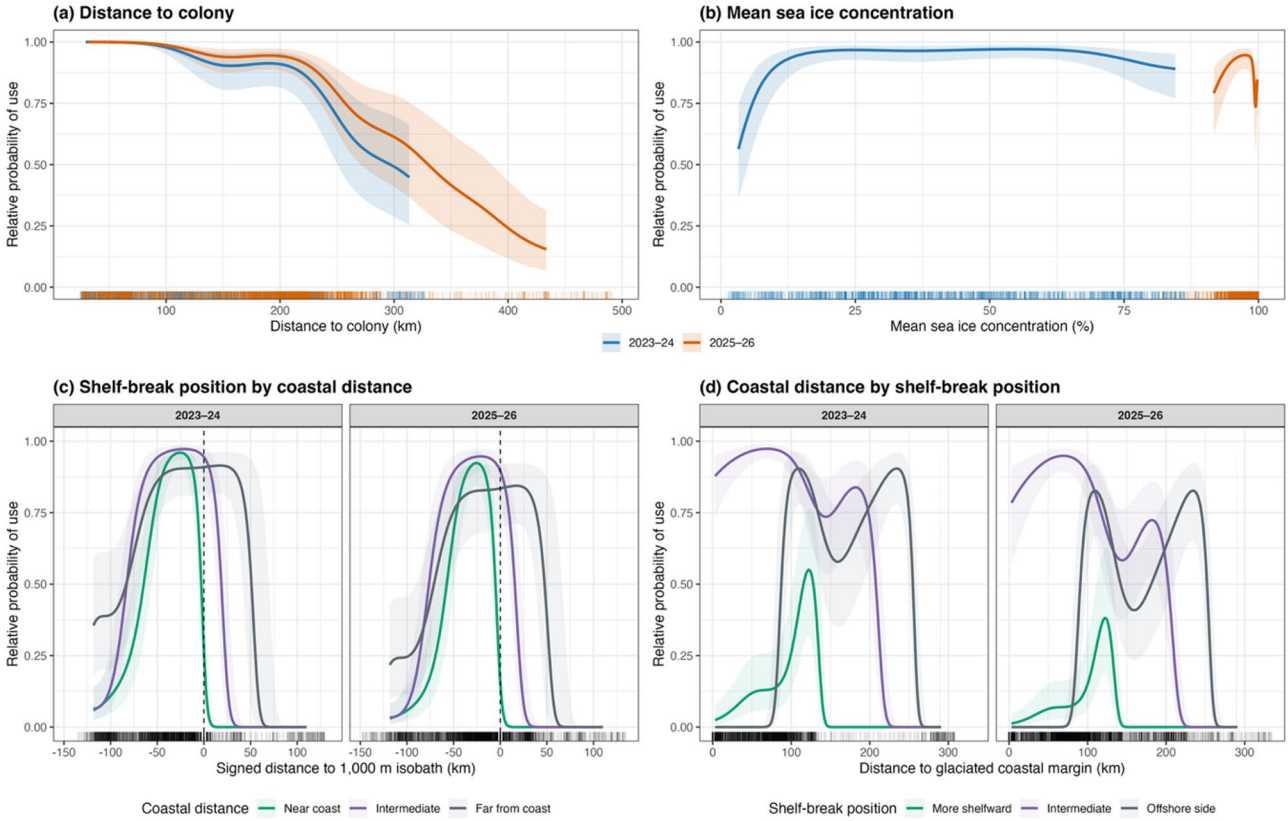


Fig. 4. Conditional predictions from the selected population level habitat-selection GAM for breeding emperor penguins during chick-rearing. Panels show predicted relative probability of use in relation to (**a**) distance to the colony, (**b**) mean sea ice concentration, (**c**) signed distance to the 1,000 m isobath conditional on distance to the glaciated coastal margin, and (**d**) distance to the glaciated coastal margin conditional on signed distance to the 1,000 m isobath. Predictions in panels (**a**) and (**b**) are shown for the 2023-24 and 2025-26 study years, with non-focal covariates held at study-year specific median values from used locations. In panels (**c**) and (**d**), curves represent conditional slices through the fitted tensor interaction at representative values drawn from the distribution of used locations. Bird and trip level random effects were excluded from all population-level predictions. Shaded areas show approximate 95% confidence intervals, and rug marks indicate observed used locations. For signed distance to the 1,000 m isobath, negative values indicate shallower shelf waters and positive values indicate deeper offshore waters.

Discussion

During the chick-rearing period, breeding emperor penguins must forage at sea while returning regularly to the colony to provision chicks, so the location and predictability of foraging areas are central to breeding ecology[26,27]. Previous tracking studies have shown that breeding emperor penguins often use shelf, slope and sea ice-associated habitats, where bathymetry and access features such as leads, cracks and polynyas can structure foraging opportunities[17,27,28,35]. Our study extends this understanding to Snow Hill Island, the northernmost known emperor penguin colony, and provides the first characterisation of chick-rearing space use, habitat associations and at-sea behaviour for breeding emperor penguins in the northwestern Weddell Sea. Across two contrasting sea ice conditions in 2023-24 and 2025-26, emperor penguins breeding at Snow Hill repeatedly used a broad region east and northeast of the colony, aligned with the shelf-break associated sector of the northwestern Weddell Sea, while a subset of individuals also used waters close to glaciated coastal margins along the eastern Antarctic Peninsula. This pattern is consistent with previous evidence that emperor penguins use shelf and sea ice associated foraging habitats but adds two important insights: the population showed broad spatial recurrence in the same geographical foraging region across contrasting sea ice conditions, while individual tracks also revealed variation in the use of offshore shelf-break associated, coastal and iceberg associated areas. Together, these findings suggest that chick-rearing emperor penguins at Snow Hill Island use a structured foraging landscape shaped by bathymetry, sea ice conditions and local coastal or iceberg associated features.

Breeding emperor penguins from Snow Hill Island repeatedly used a broad foraging region east and northeast of the colony across both chick-rearing study years. This pattern was clearest at the scale of the overall foraging range, rather than the exact position of the core-use areas. Although both study years showed broad spatial recurrence, the highest-use areas shifted or expanded within this region in 2025-26, when trips were longer and space use was broader. This suggests that breeding emperor penguins did not simply use identical areas between

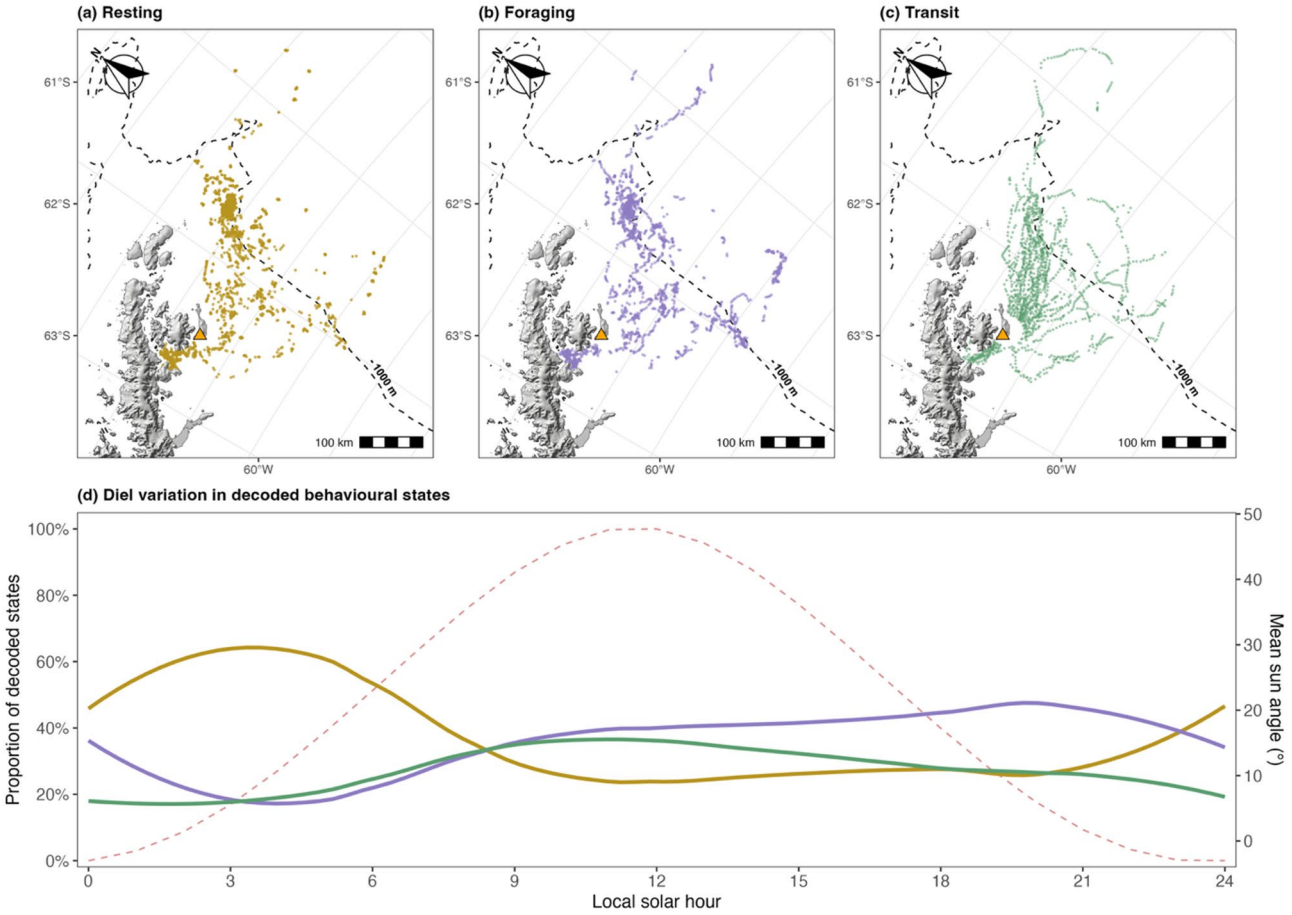


Fig. 5. Spatial and diel patterns of behavioural states identified by the best-supported Hidden Markov Model during chick-rearing trips of breeding emperor penguins from Snow Hill Island. Top panels show locations classified as (**a**) resting, (**b**) foraging and (**c**) transit. The orange triangle marks the colony location, and the dashed black line indicates the − 1,000 m isobath, used here as a proxy for the continental shelf-break. Panel (**d**) shows diel variation in the proportion of decoded locations assigned to each behavioural state across local solar hour, with coloured lines representing resting, foraging and transit. The red dashed line and right-hand axis show mean hourly sun angle for visual reference only.

years but showed recurrent population-level use of the same general foraging region, with differences in the precise location and extent of use between study years.

The repeated use of this region appears to reflect more than a simple effect of distance from the colony, with the habitat-selection model helping clarify which environmental features were associated with this site fidelity. It supported the importance of shelf-break position, sea ice context and distance to glaciated coastal margins, providing stronger support for the interpretation already suggested by the tracks: that Snow Hill breeders were repeatedly using a structured foraging landscape associated with the northwestern Weddell Sea shelf-break system. This is consistent with the spatial pattern visible in the tracks, where penguins repeatedly moved towards the shelf-break associated region east and northeast of Snow Hill Island, close to the transition between the northwestern Weddell Sea shelf and the bathymetric structures bordering the Powell Basin. Such shelf-edge and canyon-like features may enhance prey availability by structuring currents, water masses and prey aggregation, potentially creating predictable foraging opportunities for predators[36,37].

This association with shelf/slope waters is consistent with previous studies showing that emperor penguins frequently use continental shelf and upper-slope environments during chick-rearing. For example, at the Auster colony in East Antarctica, emperor penguins foraged mainly over shelf waters of approximately 200–500 m depth, while chick-rearing birds from Pointe Géologie generally remained associated with shelf areas and rarely extended beyond the shelf slope[27,35]. Similarly, studies from other regions have shown that emperor penguins use sea ice habitats that occur over continental shelves, often exploiting access features such as leads, cracks and polynyas[17,28].

Moreover, this broad pattern did not describe all individual tracks equally. The population-level habitat model indicated higher predicted use in two contrasting settings: shallower shelf waters closer to glaciated coastal margins and more offshore, shelf-break associated waters. Visual inspection of individual tracks also showed variation among birds in their use of these areas (Fig. S1). Such individual variation is consistent with broader evidence that seabirds and other central-place marine predators within the same population can

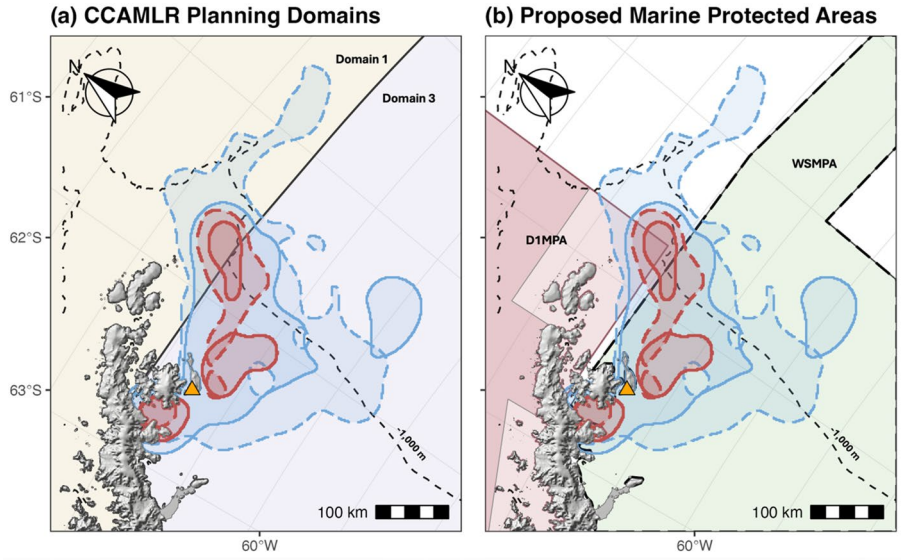


Fig. 6. Spatial relationship between chick-rearing foraging areas and conservation-planning boundaries. Study-year kernel utilisation distributions (UDs) for breeding emperor penguins from Snow Hill Island are shown relative to (**a**) Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) Planning Domains 1 ("Western Antarctic Peninsula–South Scotia Arc") and 3 ("Weddell Sea"), and (**b**) the proposed Weddell Sea Marine Protected Area (WSMPA) and proposed Western Antarctic Peninsula and South Scotia Arc Marine Protected Area (Domain 1 MPA). Within panel (**b**), the D1MPA includes the General Protection Zone and Krill Fishing Zone, while the mapped portion of the WSMPA corresponds to the General Protection Zone. In both panels, 50% UDs are shown in red and 95% UDs in blue; solid outlines indicate 2023-24 and dashed outlines indicate 2025-26. The orange triangle marks the Snow Hill Island colony, and the black dashed line indicates the − 1,000 m isobath, used here as a proxy for the continental shelf-break.

specialise in different foraging areas, habitats or prey types[38–41]. Most penguins from Snow Hill Island were primarily associated with shelf-break associated waters east and northeast of the colony, but a smaller west to northwest component towards the Prince Gustav Channel region suggests that some individuals also exploited nearshore coastal waters along the eastern Antarctic Peninsula. In colonial central-place foragers, spatial or habitat specialisation may reduce overlap among individuals and relax local competition around breeding colonies, particularly where many individuals repeatedly exploit the same broad foraging region during chick-rearing[42,43]. This coastal component appeared to be associated with waters close to the glaciated coastal margins of the Sjögren-Boydell glacier system. Given the small number of individuals, this pattern should be interpreted cautiously but suggests that coastal waters may represent an additional foraging option rather than a replacement of the principal east-northeastern shelf-break associated region. Glacially influenced coastal waters can enhance local productivity or prey aggregation through meltwater inputs, stratification and local hydrographic processes, and may therefore provide local foraging opportunities for some individuals[44,45].

Furthermore, the large icebergs A81 and D33A, located southwest of the colony during the 2025-26 study year, may have influenced movement routes within the broader foraging landscape (Fig. S3). The close circling behaviour of at least three individuals (43643, 43644 and 43648) suggests that iceberg edges may have been used as local foraging features, rather than acting only as obstacles. Large icebergs can modify habitat structure, access routes, hydrography and nutrient dynamics[46], and previous work in the Ross Sea showed that giant icebergs affected emperor penguin colonies by blocking usual access routes to breeding areas[47]. This interpretation is also consistent with reports of seabird aggregations around free-drifting icebergs in the northwest Weddell and Scotia Seas[48]. In our study, we could not separate the effects of A81 and D33A from those of denser sea ice, but the movement of several tracks around these icebergs suggests that local ice features may have contributed to longer or more indirect routes, and possibly to the broader offshore distribution observed in 2025-26.

Sea ice concentrations changed the context in which this recurrent foraging region was used. In 2025-26, core-use areas occurred in much denser pack ice than in 2023-24, and trips were longer, although the study-year effect on trip duration was not retained after correction for multiple testing. This difference does not necessarily indicate that penguins selected a different geographical foraging region, but rather that the recurrent shelf/slope associated region was positioned differently relative to the marginal ice zone between years. In 2023-24, this region was closer to the marginal ice zone and partly beyond the 5% SIC contour (outer low-concentration ice margin), whereas in 2025-26 it was embedded within dense pack ice as this margin occurred farther north. Rather than indicating direct energetic costs, which we did not measure, this pattern may reflect reduced permeability of the foraging landscape under denser sea ice. In dense or consolidated pack ice, access to open water, breathing opportunities and movement corridors is structured by leads, cracks and polynyas, which can influence how emperor penguins move between the colony and foraging areas[17,28]. Overall, our results indicate

repeated use of a shelf/slope-associated foraging region under contrasting sea ice conditions, with flexibility in core-use areas, routes and individual use of waters close to glaciated coastal margins between years.

The HMM results showed that at-sea behaviour of breeding emperor penguins from Snow Hill Island varied in relation to both sea ice concentration and local time. Resting and foraging occurred in more ice-covered areas than transit. This suggests that denser pack ice was associated with areas where penguins slowed movement and increased localised activity, but this pattern should not be interpreted only in terms of prey availability. Sea ice may also influence behaviour by structuring movement permeability, access to breathing sites and exposure to predators. In consolidated or dense pack ice, leads, cracks and small polynyas can provide essential access points between the ice surface and the water column, allowing penguins to rest, breathe and forage within otherwise continuous ice cover[17,28]. At the same time, the distribution of these access points may affect perceived risk, because penguins moving through open water or repeatedly using restricted breathing holes may differ in their exposure to predators, such as leopard seals *Hydrurga leptonyx* or killer whales *Orcinus orca*. Predator effects on penguin movement are often non-consumptive, influencing habitat use, route choice and time allocation even when predation events are not directly observed[49,50]. Transit through lower sea ice concentrations may therefore reflect movement through more permeable parts of the pack, including leads, cracks or lower-ice corridors, but may also involve faster movement through more exposed areas. Although predator presence was not measured here, these patterns suggest an association between sea ice conditions and not only where emperor penguins slowed and increased localised activity, but also how they moved between the colony and foraging areas.

Combining decoded at-sea behavioural states with colony-attendance intervals placed these patterns in the broader chick-rearing cycle. As central-place foragers, breeding emperor penguins must balance time at sea with repeated returns to the colony to provision chicks, and previous studies have shown that foraging-trip duration and activity budgets vary through chick-rearing as chick demand changes[26,27,51]. In our study, the difference in the full trip-cycle time budget between study years reflected a greater proportion of time at sea in 2025-26, while mean inter-trip colony attendance was similar between years.

The diel pattern in decoded states further suggests that emperor penguin behaviour varied with the local light environment. Foraging increased during the evening, reaching its highest proportions between 19:00 and 21:00, whereas resting peaked during the early morning and transit was most common around midday. This pattern is consistent with previous studies showing that emperor penguins adjust foraging and diving activity in relation to light conditions[27,52–54]. As visual predators, emperor penguins depend on sufficient light to detect prey, but at Snow Hill Island during late spring, twilight conditions may still allow visual hunting while coinciding with increased prey accessibility closer to the surface, as shown in previous penguin studies[55].

The evening increase in inferred foraging in our study may therefore reflect an interaction between light availability and prey behaviour. Many Antarctic prey species, including Antarctic silverfish *Pleuragramma antarctica*, Antarctic krill *Euphausia superba* and squid such as *Psychroteuthis glacialis*, are key components of emperor penguin diet[56–59], and can show diel changes in vertical distribution, with prey becoming more accessible in shallower waters during darker periods. Under the long daylight conditions experienced during chick-rearing at Snow Hill Island, penguins may experience sufficient light for visual foraging while benefiting from prey movement towards shallower depths during the evening[60]. Together, these results suggest that the timing and spatial distribution of resting, transit and foraging states varied in relation to both sea ice structure and diel conditions. Such flexibility may be particularly important at the northern limit of the species' breeding distribution, where environmental conditions vary substantially between years and access to profitable foraging areas may depend on the shifting distribution of sea ice and prey.

The recurrent use of shelf-break associated foraging habitats, together with use of waters close to glaciated coastal margins and iceberg associated features, is relevant to spatial conservation planning in the Weddell Sea and adjacent Antarctic Peninsula region. The proposed WSMPA encompassed much, but not all, of the chick-rearing habitat used by breeding emperor penguins from Snow Hill Island, with the overlapping areas occurring within the proposed General Protection Zone[61,62]. Smaller but consistent overlap also occurred with the proposed D1MPA, particularly for the 2025-26 core-use area. These overlaps should be interpreted as evidence of planning relevance rather than as direct evidence of effective protection. Both MPAs remain proposed rather than implemented, and the extent to which their designation would directly reduce risks to emperor penguins in this region remains uncertain, particularly where current human activity is limited by persistent sea ice cover and where the dominant long-term threat is climate-driven change in sea ice habitat[7,12,24]. Nevertheless, the occurrence of recurrent foraging areas both within and beyond the proposed MPA boundaries provides a spatial baseline for evaluating how conservation-planning frameworks encompass habitats used during a key stage of the breeding cycle. Because these areas extended across CCAMLR Planning Domains 1 and 3, future spatial assessments should consider Snow Hill Island chick-rearing habitat in relation to both Weddell Sea and Antarctic Peninsula conservation-planning scenarios. This is particularly relevant because MPA planning and broader marine spatial planning are complementary but distinct processes, whose integration may become increasingly important in the Southern Ocean under climate change[63].

As one of the northernmost emperor penguin colonies, Snow Hill Island also provides a valuable monitoring site for assessing how breeding emperor penguins respond to increasingly variable sea ice conditions. The variation among individual tracks observed here suggests that monitoring should consider not only colony-level foraging distributions, but also whether different patterns of habitat use respond differently to changing sea ice, glaciated coastal-margin and iceberg conditions. More broadly, by identifying recurrent at-sea habitats and the environmental conditions associated with their use, these results contribute spatially explicit evidence to support precautionary conservation measures for emperor penguins, including their continued consideration as an Antarctic Specially Protected Species under the Antarctic Treaty System[14]. This is especially relevant following the species' reclassification as Endangered on the IUCN Red List, driven by projected population declines linked

to climate-driven sea ice change[15], and recent evidence that emperor penguin population dynamics are sensitive to sea ice fluctuations[24].

Although behavioural states were inferred from horizontal movement and wet/dry data, and fine-scale sea ice features, such as leads, cracks and small polynyas, could not be fully resolved, the patterns identified here were consistent across two contrasting study years with noticeably different sea ice conditions. Future work combining multi-year tracking, dive behaviour, prey-field information and higher-resolution sea ice data would help refine understanding of how emperor penguins use shelf/slope associated habitats under changing sea ice conditions, and whether individual use of waters close to glaciated coastal margins or iceberg associated features reflects persistent specialisation or opportunistic responses to local conditions. Future comparisons across colonies would also help determine whether the responses observed at Snow Hill Island are consistent with broader demographic responses to sea ice variability[64]. Importantly, such work should strengthen the implementation and evaluation of conservation measures rather than be viewed as a prerequisite for action. Overall, this study shows that breeding emperor penguins from Snow Hill Island repeatedly used a geographically constrained but environmentally variable foraging region, spanning shelf-break associated habitats east and northeast of the colony and a smaller nearshore coastal component along the eastern Antarctic Peninsula. By linking movement patterns to sea ice structure, bathymetric features, glaciated coastal margins, iceberg associated habitat use and conservation-planning boundaries, these findings strengthen the ecological basis for precautionary conservation action for emperor penguins in a rapidly changing sector of the Southern Ocean.

Methods

Study site, deployment period and tagging procedures

Our study was conducted at the emperor penguin colony on the southwestern side of Snow Hill Island (64° 31′ S, 57° 16′ W), northern Weddell Sea, Antarctica (Fig. 1). Access to the colony was achieved either by helicopter from an icebreaking research vessel or by disembarking directly from the icebreaker onto the sea ice platform and walking to the colony.

Satellite Platform Transmitter Terminals (PTTs; model SPOT-367, Wildlife Computers, USA) were deployed on adult emperor penguins during chick-rearing. In 2023, 15 individuals were tagged over two fieldwork days, on 16 and 17 November. In 2025, nine individuals were tagged during two deployment periods: five on 20 November and four on 29 November. One tag deployed in 2025 failed shortly after deployment and was excluded from subsequent analyses. All transmitters included saltwater immersion sensors to record the percentage of wet-dry time between hourly intervals. Tags were attached to the lower back feathers using waterproof Tesa® tape and epoxy resin, following established protocols designed to minimise hydrodynamic drag and behavioural disturbance[65].

Breeding status was inferred from repeated returns to the colony during chick-rearing, consistent with parental care. Individuals were classified as breeders if they repeatedly returned to the colony until the final departure from the colony associated with chick fledging. Across both study years, nine individuals were inferred to be breeders and retained for subsequent analyses: four in 2023-24 and five in 2025-26.

All animal handling, capture, and tagging procedures were approved by the British Antarctic Survey Animal Welfare and Ethics Review Board (BAS AWERB) and by the Comité de Bioética, Seguridad, Cuidado y Uso de Animales of the Millennium Institute Biodiversity of Antarctic and Subantarctic Ecosystems (BASE; approval/reference No. 1/CBSCUA/2024). Procedures were conducted in accordance with the relevant animal-welfare guidelines. Fieldwork was undertaken under UK permits BAS-S7-2023/09 and No. 11/2025–2026, and Chilean permit No. 00213/2025/2025. No anaesthesia was administered, and no animals were euthanised during the study. All procedures complied with applicable Antarctic environmental-protection and species-conservation requirements, and disturbance was minimised during capture, handling, and tagging.

Tracking data acquisition and filtering

The tracking data analysed covered the period from deployment until breeding emperor penguins left the colony for the final time before their pre-moult dispersal. Raw ARGOS locations were filtered by removing Z-class positions and applying a speed-distance-angle filter using the R package argosfilter to exclude biologically implausible locations[66]. Duplicate timestamps were resolved using a 1-second offset, and only positions with valid ARGOS error ellipses were retained. ARGOS diagnostic error ellipses, including semi-major and semi-minor axes and orientation, were incorporated to model spatial uncertainty following state-space and continuous-time movement modelling approaches[67,68]. Modelled ARGOS location estimates have an approximate accuracy of 5 km[69].

Saltwater immersion data and a 25 km radial buffer around the colony centroid were used to distinguish at-sea from on-colony periods, with the latter interpreted as stationary behaviour[70,71]. This threshold was selected a priori because it encompassed the colony and associated sub-colonies on the fast-ice platform and approximately matched the distance from the colony centroid to the nearest fast-ice edge during deployment. Locations within this buffer were interpreted as colony attendance rather than foraging movements.

Filtered data were interpolated at 1-hour intervals using a continuous-time correlated random walk model implemented in the R package crawl[68,72]. Wet/dry activity data were incorporated to distinguish stationary from moving individuals, with the 1 h interval matching the wet/dry activity bins to align movement estimates with behavioural state classification. Posterior simulations were generated using crwSimulator in crawl to account for uncertainty around estimated paths. To approximate local solar time for subsequent diel analyses, Coordinated Universal Time (UTC) was adjusted according to the longitude of each interpolated location using a correction of four minutes per degree of longitude, corresponding to the Earth's rotation of 360° in 24 h (15° h^{-1}). Thus, no correction was applied at 0° longitude, whereas locations at 60°W were adjusted by -240 min (4 h) relative to UTC.

Foraging trip segmentation

Foraging trips were identified using the R package track2KBA[73], based on the on-colony and at-sea classifications described above. The analysis was restricted to individuals inferred to be breeders that left and returned to the colony during the chick-rearing period. Complete foraging trips were defined using the tripSplit function as excursions that began and ended when individuals crossed the 25 km colony buffer defined above and lasted at least 4 h. This duration was used to exclude brief crossings of the buffer boundary that were unlikely to represent complete foraging excursions, including short local movements around the fast-ice edge or crossings associated with residual positional uncertainty. Across the nine breeding individuals retained for analysis, 38 complete foraging trips were identified. For each trip, we calculated trip duration, total distance travelled and maximum distance from the colony. For consecutive complete trips, we also calculated inter-trip colony attendance to estimate the proportion of the observed chick-rearing trip cycle spent at the colony versus at sea. As multiple trips were recorded from the same individuals, differences between study years in these four metrics were assessed using separate linear mixed-effects models, with study year as a fixed effect and individual as a random intercept. Response variables were log-transformed before modelling, and p-values were adjusted across the four comparisons using the Holm method. Trip metrics were also summarised at the individual and study-year levels.

Space-use estimation and interannual overlap

To assess recurrent space use by breeding adults during chick-rearing, we estimated kernel utilisation distributions (KUDs) using the R package adehabitatHR[74]. Kernel density estimates were based on interpolated locations from complete returned foraging trips. Individual UDs were first estimated using a common bandwidth and spatial grid. Each individual UD was normalised to integrate to one, and the study-year UD was then calculated as the cell-wise arithmetic mean of the normalised individual UDs, giving each bird an equal contribution irrespective of the number of tracking locations or trip duration. The 50% and 95% isopleths were extracted to represent core-use areas and the broader foraging range during chick-rearing, respectively.

Overlap between study years was quantified using Bhattacharyya's affinity (BA) and the utilisation distribution overlap index (UDOI), calculated from the continuous utilisation distributions following the definitions implemented in adehabitatHR[74,75]. BA was calculated using the full continuous UDs and used as an overall measure of similarity between study years, whereas UDOI was calculated for the 50% and 95% UDs to compare overlap in the intensity of space use within core-use areas and the broader foraging range, respectively.

Environmental data and habitat-selection modelling

Environmental covariates potentially associated with foraging habitat use were compiled. Daily sea ice concentration (SIC) was obtained from University of Bremen satellite-derived products (~ 3.125 km spatial resolution, https://data.seaice.uni-bremen.de/databrowser/;[76]. For visualising broad interannual sea ice context, a December median SIC raster was calculated for each study year by taking the median SIC at each grid cell across all daily rasters from 1 to 31 December 2023 and 1 to 31 December 2025, respectively. This month represented the main chick-rearing foraging period covered by the tracking data, while the median reduced the influence of short-term daily variability. A 5% SIC contour was also extracted to represent the outer low-concentration ice margin and was used only to provide spatial context for penguin movements relative to the marginal ice zone.

For habitat-selection modelling, daily SIC rasters covering the chick-rearing tracking period in each study year (from 17 November to 28 December 2023 and from 23 November 2025 to 15 January 2026) were projected, cropped and masked to the availability domain. This was delineated using a radial buffer around the colony that was 10% larger than the maximum observed distance from the colony. For each study year, SIC was summarised at each grid cell across these daily rasters as the mean, standard deviation, minimum and maximum.

Bathymetry was derived from the IBCSO gridded bathymetric dataset[77] and resampled to match the spatial scale of the sea ice data. From these data, we derived depth, bathymetric slope, distance from the colony, and distance from the 1,000 m isobath. We additionally calculated signed distance from the 1,000 m isobath, with negative values representing the shallower shelf side and positive values the deeper offshore/slope side, allowing broad position relative to the continental shelf-break to be represented explicitly. The 1,000 m isobath was used as a proxy for the continental shelf-break in this part of the Weddell Sea. Distance to glaciated coastal margins was calculated using the Global Land Ice Measurements from Space (GLIMS) Glacier Database[78]. This predictor was included because tracks from both study years showed that some individuals repeatedly used waters close to these glaciated coastal margins, contrasting with the more offshore shelf-break associated areas used by other individuals.

Interpolated locations from complete chick-rearing foraging trips outside the colony buffer were used as used locations. Prior to generating available locations, used locations were restricted to those with complete environmental covariate information. Available locations were then sampled randomly from ocean cells within the corresponding year-specific availability domain at a ratio of three available locations per used location within each trip. Trip and bird identities were retained for both used and available locations. Environmental covariates were extracted for all locations, continuous predictors were scaled, and candidate predictors were assessed for collinearity.

We fitted binomial generalised additive models (GAMs) using the R package mgcv[79] with used versus available location as the response. Continuous environmental covariates were represented using penalised smooth terms because we had no ecological basis for assuming strictly linear habitat responses; for example, responses to SIC, distance from the colony or position relative to the shelf edge could plausibly contain thresholds, plateaus or intermediate ranges of higher use. Smooth complexity was constrained using predefined basis dimensions and penalisation during model fitting. Bird identity and trip identity (with trips nested within birds) were included as random intercepts in all population-level candidate models to account for repeated observations within birds and trips.

Candidate models were fitted using maximum likelihood and compared using AIC, deviance explained, and inspection of the resulting response and prediction surfaces. Distance from the colony was retained throughout as a central-place constraint. Initial candidate models evaluated sea ice and bathymetric covariates individually and additively. Based on the recurring spatial pattern apparent in both study years, in which some birds used offshore shelf-break associated areas whereas others made greater use of waters close to glaciated coastal margins, we further evaluated whether position relative to the 1,000 m isobath interacted with proximity to the glaciated coastal margin. This formulation was compared with models containing the same variables individually or additively, as well as equivalent depth-based additive and interaction models. The best-supported population model was subsequently refitted using restricted maximum likelihood for inference, diagnostics and prediction.

Temporal dependence was evaluated separately from the hierarchical random-effect structure. Within-trip autocorrelation in the environmental covariates was examined across increasing temporal lags, and robustness of the habitat-selection results was assessed by repeating the population-level analysis after thinning used locations to 6, 12 and 24 h intervals. Available locations were regenerated within trips at the same 3:1 ratio for each thinned dataset, and the selected tensor formulation was compared with the corresponding additive model at each temporal resolution. Spatial predictions from the thinned models were also compared with those obtained from the hourly data.

Finally, leave-one-individual-out cross-validation was used to assess whether the selected population-level model generalised to birds excluded from model fitting. Each bird and all of its associated trips were removed in turn, the model was refitted to the remaining individuals, and predictions were generated for the held-out bird using the population-level environmental component of the model; bird- and trip-specific random effects were excluded because these effects cannot be estimated for previously unseen individuals or trips. Predictive discrimination was assessed using the area under the receiver operating characteristic curve (AUC), sensitivity and specificity. Fitted values from the final model were interpreted as relative probability of habitat use.

Behavioural state modelling

To classify movement behaviour during chick-rearing, we fitted Hidden Markov Models (HMMs) using the R package momentuHMM[80]. Models were fitted to hourly interpolated locations from complete returned breeder trips, and step length, turning angle and proportion of time immersed were used as response variables. Step lengths were modelled using Weibull distributions, turning angles using wrapped Cauchy distributions, and proportion of time immersed (ω) using beta distributions with a zero-mass component for intervals with no recorded immersion. Time immersed was derived from the tags' saltwater immersion data and included to help distinguish resting from foraging behaviour, as both states can involve short movements and low directional persistence.

A three-state HMM was fitted a priori for ecological interpretability: 'resting' (low displacement, high dry proportion, and limited directional persistence), 'transit' (long step lengths and directed movement), and 'foraging' (shorter step lengths, high turning angles, and high wet proportion consistent with area-restricted search).

State transition probabilities were modelled as a function of covariates expected to influence movement behaviour during chick-rearing. Candidate covariates included local solar time, modelled as a 24 h periodic effect using a cosinor term, and sea ice concentration (SIC). Candidate transition models included local solar time and SIC fitted singly, additively, and with an interaction, and model support was compared using AIC.

Decoded HMM state durations were summarised as proportions of at-sea time and, where combined with colony-attendance estimates, were rescaled relative to the full observed trip cycle.

Spatial overlap with conservation-planning boundaries

To assess the extent to which proposed MPAs encompass foraging areas during chick-rearing, we quantified area overlap between the 50% and 95% UDs for each study year and the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) MPA Planning Domains, obtained from the CCAMLR GitHub repository. We also quantified overlap with the proposed Weddell Sea Marine Protected Area (WSMPA) and the proposed Western Antarctic Peninsula and South Scotia Arc Marine Protected Area (Domain 1 MPA; D1MPA), obtained from the MPAtlas summary database (Marine Conservation Institute; May 2026 release;[62]. For each proposed MPA, the management zones were dissolved into a single polygon before calculating total MPA overlap, avoiding double-counting among overlapping zone geometries.

Land and coastline layers were obtained from the Scientific Commission on Antarctic Research (SCAR) Antarctic Digital Database[81–83], and land shaded relief was derived from the Reference Elevation Model of Antarctica (REMA)[84].

All analyses and figures were produced in R version 4.5.1[85], using the ggplot2, sf, terra, ggspatial and associated R packages.

Data availability

The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

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Author contributions

H.R.G., N.R., P.F.T. and J.C.X. designed the study. H.R.G. conducted the analyses and wrote the manuscript, with methodological support from V.W.E. on habitat-selection modelling. N.R., P.F.T. and J.C.X. supervised the study and contributed to manuscript development. H.R.G., N.R., P.F.T., K.P., G.D., J.A.V., E.J.P., L.K. and N.E.O. partic-

ipated in fieldwork and contributed to data collection. All authors reviewed and approved the final manuscript.

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Declarations

Competing interests
The authors declare no competing interests.

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Correspondence and requests for materials should be addressed to H.R.G.

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