Landsc Ecol (2025) 40:78
https://doi.org/10.1007/s10980-025-02088-y

RESEARCH ARTICLE

Long-term, landscape- and wind-driven snow conditions influence Adélie penguin colony extinctions

Megan A. Cimino · **Gregory D. Larsen** · **David W. Johnston** · **Dulcinea V. Groff**

Received: 12 July 2024 / Accepted: 18 March 2025 / Published online: 3 April 2025

Abstract

Context The interaction between topography and wind influences snow cover patterns, which can determine the distribution of species reliant on snow-free habitats. Past studies suggest snow accumulation creates suboptimal breeding habitats for Adélie penguins, leading to colony extinctions. However, evidence linking snow cover to landscape features is lacking.

Objectives We aimed to model landscape-driven snow cover patterns, identify long-term weather changes, and determine the impact of geomorphology and snow conditions on penguin colony persistence.

Methods We combined remotely sensed imagery, digital surface models, and > 30 years of weather data with penguin population monitoring from 1975 to 2022 near Palmer Station, west Antarctic Peninsula. Using a multi-model approach, we identified landscape factors driving snow distribution on two islands. Historic and current penguin sub-colony perimeters were used to understand habitat selection, optimal habitat features, and factors associated with extinctions.

Results Decadal and long-term trends in wind and snow conditions were detected. Snow accumulated on lower elevations and south-facing slopes driven by the north-northeasterly winds while Adélie penguins occupied higher elevations and more north-facing slopes. On Torgersen Island, sub-colonies on south aspects have gone extinct, and only five of the 23 historic sub-colonies remain active, containing 7% of the 1975 population. Adélie penguins will likely be extinct on this island in < 25 years.

Conclusions Adélie penguin populations are in decline throughout the west Antarctic Peninsula with multiple climate and human impacts likely driving Adélie penguins towards extinction in this region. We demonstrate precipitation has detrimental effects on penguins, an often overlooked yet crucial factor for bird studies.

Keywords Landscape effects · Penguin · Geomorphology · Antarctic · Extinction · Snow

---

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s10980-025-02088-y.

M. A. Cimino (✉)
Ocean Sciences Department, Institute of Marine Sciences, University of California Santa Cruz, Santa Cruz, CA, USA
e-mail: mecimino@ucsc.edu

G. D. Larsen
Department of Biology, Wake Forest University, Winston-Salem, NC, USA

D. W. Johnston
Nicholas School of the Environment, Duke University Marine Laboratory, Beaufort, NC, USA

D. V. Groff
Department of Geology and Geophysics, University of Wyoming, Laramie, WY, USA

Introduction

Interactions amongst precipitation patterns, terrain features, and wind can shape meso- to microclimates, impacting organisms' terrestrial habitats and their ability to survive and function (Trew and Maclean 2021). In mountainous regions or areas of complex topography, wind can redistribute snow cover (Dadic et al. 2010), particularly through snow drift, characterized by intensified wind speeds eroding snow on the windward side of ridges and decreased wind speeds facilitating snow deposition on the leeward side (Radok 1977; Pomeroy et al. 1997; Liston and Sturm 1998). Furthermore, wind can increase turbulent heat fluxes to snow cover (Marks and Winstral 2001), influencing the timing and magnitude of snowmelt runoff. Given that climate projections indicate increased precipitation in warming polar regions, identifying drivers of snow cover patterns across uneven terrain is important (McCrystall et al. 2021; Tewari et al. 2022). Moreover, identifying potential shifts in snow distribution can aid in anticipating consequences on species distribution, abundance, and productivity patterns that rely on snow-free habitats.

In regions with spatially heterogeneous snow accumulation, animal and vegetation distributions can become patchy because biological processes are influenced by the seasonal snow cycle. In the Arctic, snow is a climatic driver of biology (Post et al. 2009) where the timing of snowmelt/advance, snowpack hardness, and length of the plant growing season impact species population dynamics from reindeer to rodents (Ananicheva et al. 2011). In the Antarctic, although terrestrial species diversity is lower, precipitation remains a key factor influencing species distributions (Convey et al. 2014; van de Pol et al. 2017), including plants (Favero-Longo et al. 2012; Kim et al. 2016), insects (Chown and Convey 2016) and upper trophic levels. Many seabird and seal species exhibit site fidelity and require snow-free terrain for molting and breeding (Cimino et al. 2023a). Drier conditions enhance breeding success by preventing snowfall and puddles from covering rocky or organic nesting materials (Descamps et al. 2023). Further, wetting can increase thermoregulatory costs for seabird chicks and seal pups, and impact survival rates (Chapman et al. 2011; McDonald et al. 2012; Ropert-Coudert et al. 2015; Pearson et al. 2022). Therefore, identifying habitats prone to snow accumulation can aid in predicting species responses.

The west Antarctic Peninsula (AP) is rapidly warming with reduced sea ice, increased snowfall (Thomas et al. 2008, 2017; Eayrs et al. 2021; Fogt et al. 2022) and snow cover can be redistributed by wind and topographic dynamics (Van Lipzig et al. 2004; Dattler et al. 2019). One objective of the Palmer Antarctica Long-Term Ecological Research program is to identify mechanisms behind the population decline of breeding Adélie penguins (*Pygoscelis adeliae*), a key Antarctic indicator species. Adélie penguins experience the same regional-scale changes in climate and sea ice, but sub-populations on five islands near Palmer Station have declined at different rates (Fraser et al. 2013). Hillshade modeling of these islands suggested that Litchfield Island, where the Adélie penguin colony went extinct in 2007, has the highest amount of suboptimal habitat, defined as the areal proportion of an island with a southwest aspect where snow would hypothetically accumulate from the dominant northeasterly winds (Fraser and Patterson 1997; Patterson et al. 2003). The interaction between island topographies, wind, and increased snow accumulation is thought to be responsible for varying population decline rates and extinctions but this theory remains to be fully tested with observational data.

Here, we investigate this long-standing hypothesis on fine-scale, wind-driven snow accumulation patterns, and specifically, that snow accumulates on southern facing landscapes creating suboptimal habitats that influence Adélie penguin population and occupancy patterns. Snow accumulation and melt patterns can be difficult to consistently measure over biologically relevant spatiotemporal scales (meters and decades). Thus, for a synoptic view, we used periodic spatial data from satellite remote sensing and unoccupied aircraft systems (UAS, or drones) with long-term snow depth measurements at snow stakes. Satellite imagery can provide relatively high-resolution coverage over large spatial areas, but darkness, clouds, and infrequent passes inhibit regular data collection in polar regions. Drones can provide higher-resolution data but require suitable weather and personnel for operations, and survey coverage is limited by battery life and regulatory factors. Snow stakes can provide daily, year-round records of snow depth but manual observation practically limits the number and frequency of measurements. By combining diverse datasets, we tested for trends in snow and wind characteristics over time, geomorphological influences on snow cover, and how geomorphology and snow cover may influence penguin colony persistence. We provide a mechanistic understanding for why some Adélie penguin sub-colonies went extinct, which has implications for penguin population trends in Antarctica and beyond.

Methods

Study site and overview

This study focuses on a region near Palmer Station, Anvers Island, where long-term penguin population monitoring has occurred periodically since 1975 (Fig. 1). The two largest local populations of Adélie penguins are on Torgersen and Humble Islands (Fraser and Patterson 1997; Fraser et al. 2013), our focal study sites.

We used multiple data sources to investigate seasonal, multidecadal and spatial patterns in snow cover and accumulation over heterogeneous landscapes, which was necessary because long-term,

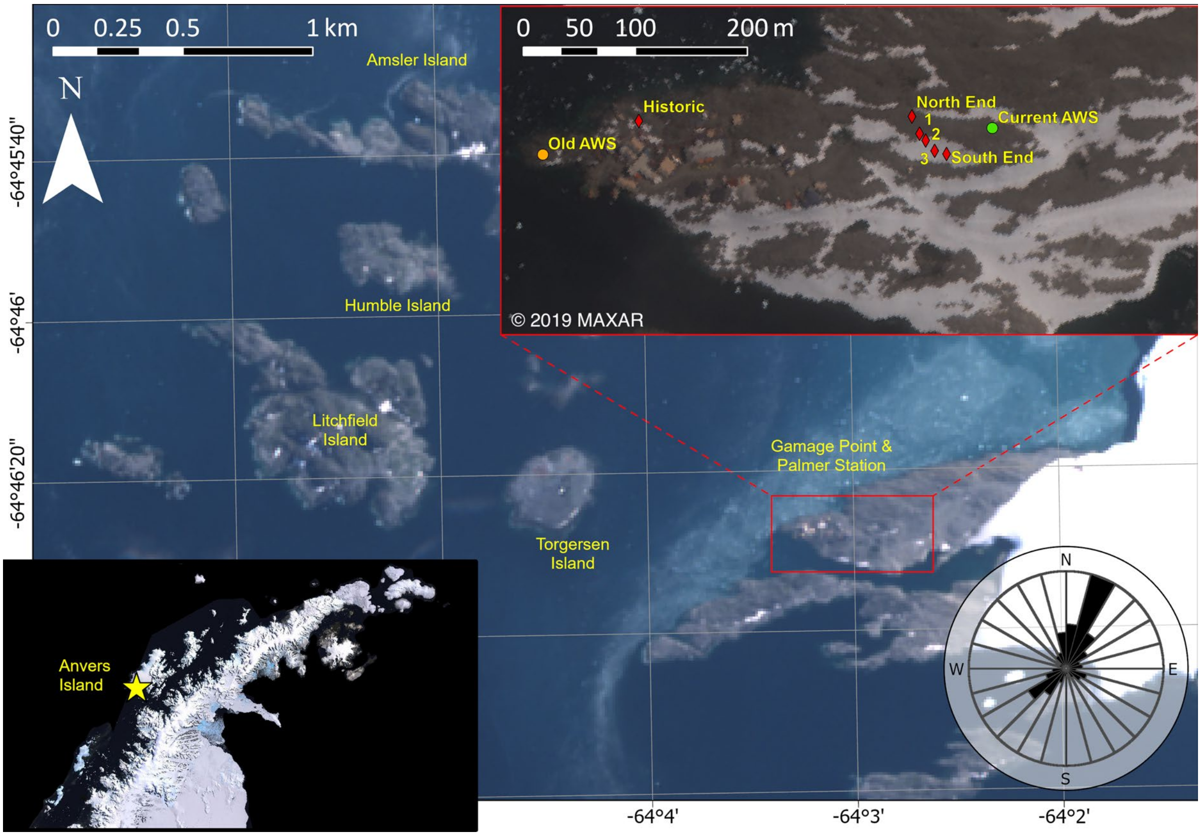

Fig. 1 Location of study sites and instrument locations near Palmer Station, Anvers Island, west Antarctic Peninsula. Focal penguin colonies are located on Torgersen and Humble Island. From 1990 to 2017, snow depth was measured at a single state ("historic"), and in 2016, five snow stakes were installed behind the station (red diamonds). From 2001 to 2017, the automated weather station (AWS) was located on Gamage Point ("Old AWS"), and in 2015, a new weather station was installed behind the station ("Current AWS"). Mean wind speed measured during the snow accumulation period from 1990 to 2022 was 6.1 m/s with a dominant north-north-east direction (bottom right). Imagery: Sentinel 2, true-color, 18 February 2020; 2008 Landsat Image Mosaic of Antarctica (bottom left); Worldview-2 image ID 103001009B50EB00 on 20 December 2019 (Copyright 2019 Maxar, top right)

fine-scale and island-specific data were not consistently available. We used > 30 years of daily weather data collected at Palmer Station to investigate trends in wind and snow depth. Drone surveys were used to create digital surface models of Torgersen and Humble Islands and to identify and model snow cover. Satellite imagery illustrated spatial patterns in seasonal snow cover in relation to penguin colony locations. We used one satellite image to determine snow cover in a high snow year for modeling snow cover, but no other satellite images were used for analyses due to inconsistent availability. Penguin sub-colony perimeters were used to investigate the relationship between past and current sub-colony locations, extinctions and habitat features. Finally, we used a time series of Adélie penguin chick fledging masses to understand chick health after snowy breeding seasons as an additional mechanism that influences recruitment into the breeding population.

A breeding season or austral spring–summer season was referred to using the first year in a split year (e.g., 1991 refers to the 1991–1992 season). We define fall as March through May (MAM), winter as June through August (JJA), spring as September through November (SON), and summer as December, and January and February of the following year (DJF).

Satellite imagery

All available satellite images within the Palmer Station region with no cloud cover were acquired from the Polar Geospatial Center. This resulted in 177 images from August to April and 2004 to 2022. The imagery was obtained from the Worldview-1, -2, -3, Quickbird-2, and Geoeye-1 sensors with minimum resolutions of 0.31–2.4 m. The frequency of satellite overpasses and availability of high-quality, cloud-free images were inconsistent; therefore, it was not possible to produce a time series of visual snow cover and melt patterns over one spring–summer season. However, from the available imagery, we show representative images of snow cover at Torgersen Island from the early spring (September) to the late summer (February), which covers the penguin breeding period.

Weather data and analyses

Since 1989, weather data has been recorded at Palmer Station, < 2 km from Torgersen and Humble Island, during which time, the methods and instruments of measurement have changed (Fig. S1). We focused on comparisons between snow depth from snow stakes, and wind speed and direction (Supplemental Information S1).

We tested for long-term trends in snow patterns using data from fall 1990 to summer 2022. We determined the mean and standard deviation in snow depth across all years, and for each year we determined the maximum snow depth, the day of year of the maximum snow depth, and the first day of the year without snow. We estimated the length of the snow accumulation period, from the first day of snow accumulation when snow depth observations no longer reach zero until the day of maximum snow depth. The ablation period began the day after maximum snow depth and ended on the first day when snow depth was zero. The snow-free season was defined as the first day when snow depth was zero until the snow accumulation period began. We also summed the number of days in which ≥ 1 cm (minimum resolution of the data) of snow accumulated during the penguin breeding season (15 November–12 February). Using linear regression, we tested for significant trends ($p < 0.05$) over time in these snow conditions, and the lengths of the accumulation, ablation, and snow-free periods.

Using the daily measurements of wind speed and direction, we calculated climatological means across years for each day of the year and the four seasons from fall 1990 to summer 2022. We calculated u and v wind vector components from wind speed and direction. Positive (negative) values for the v wind component indicate wind from the south (north) and positive (negative) values for the u component indicate wind from the west (east). Using linear regression, we tested for significant trends ($p < 0.05$) in wind conditions over time.

It is important to understand the seasonal snow cycle and how anomalous conditions in one season may cascade into the next. For example, extreme winter snowfall may impact biological processes the subsequent spring–summer, so we estimated the frequency of snowy and windy years. We defined a ‘snowy year’ as a year when a daily snow depth observation exceeded 91 cm, the 95th percentile threshold of the long-term dataset (World Meteorology Organization 2023). We summed the number of years in which the maximum snow depth exceeded 91 cm in five-year bins (1990 to 2019) and a three-year bin (2020 to 2022). We also estimated the proportion of 'windy days' during the snow accumulation period to test if snow and wind characteristics shifted together. We defined a 'windy day' as a day with a daily mean wind speed exceeding 13.3 m/s, the 95th percentile threshold of the long-term dataset. We calculated the proportion of windy days each year and the mean proportion of days in the same year bins as snowy years.

Drone surveys and digital surface model

We surveyed Torgersen and Humble Islands on 14 and 15 January 2020, respectively, using a DJI Phantom 4 Pro drone with a default camera payload. The drone system collected spectrally uncalibrated color imagery with 1–3 cm pixel^{-1} ground sample distance (GSD), which was used to create orthomosaic maps and three-dimensional terrain models using structure-from-motion techniques (Westoby et al. 2012; Nex and Remondino 2014) in Pix4D Mapper version 4.6.4 (Supplemental Information S2). We downsampled each digital surface model product to 0.2 m GSD (relevant to seabird nest sizes, Larsen et al. 2024) using bilinear interpolation in ArcGIS Pro 2.7.1. We describe all elevation data relative to the EGM96 geoid. All drone surveys were conducted under Antarctic Conservation Act permit 2020–016 and NOAA permit 14809–03.

Drone orthomosaics were spatially aligned to a satellite image using the coregistration tool and interface in ArcGIS Pro 2.7.1. A small number (~ 10) of persistent landscape features (cliffs, gulches, beaches, etc.) were identified in satellite imagery that could also be identified in higher-resolution drone imagery, and these were used as tie points to shift the drone orthomosaic paired digital surface model into alignment with the satellite image using a zero-order polynomial. The aligned orthomosaic was then overlaid and toggled over the satellite image in ArcGIS Pro to visually confirm alignment of shoreline and landscape features between products.

Island geomorphology and other features

Landscape features

We generated drone-derived raster products that may influence snow distribution and accumulation patterns, including elevation (m), slope (degrees), aspect (degrees), northness/eastness and hillshade. Because aspect is a circular variable (0–360°) that can complicate statistical analyses, we transformed aspect into northness and eastness components using cosine and sine functions, respectively, of aspect in radians. Positive (negative) values for northness indicate a north (south) facing slope and positive (negative) values for eastness indicate an east (west) facing slope.

We evaluated hillshade as an indicator of where snow was likely to accumulate following Patterson (2001) that suggested regions with "suboptimal habitat" had a southwest aspect and higher snow accumulation. Hillshading is a technique where lighting is added to a map based on slope and aspect of elevation surfaces to produce shaded topography maps by mimicking sun effects. We created a hillshade model that used elevation data and defined the azimuth (typically illumination source from the sun in degrees) as the predominant direction of the winds during storm events (10°) with an altitude of 20° (following the parameterization in Patterson (2001)). However, as the wind direction/speed can vary intra- and interannually, we computed five hillshade models with an azimuth that ranged from 350 to 30° in 10° increments. Hillshade was calculated using the 'WhiteboxTools' library in R, which utilizes Horn's method (the Lambertian reflectance model) (Lindsay 2016; R Core Team 2022; Wu and Brown 2022).

Snow cover

Snow cover was delineated using pixel-based supervised classification in ArcGIS Pro 2.7.1 to discriminate white land cover from non-white land cover, with manual revision and editing. Supervised classification was used because of the low number of target classes (snow and not-snow) and the high color contrast between these classes in Antarctica, which made this method particularly simple to employ, though many methods and algorithmic choices could achieve this first step of classification. A single analyst made manual edits to remove misclassified pixels, which were identified based on their location, and often consisted of waves and ice at the shoreline interface. ArcGIS Pro provided the classification and editing tools with a visual interface to facilitate visual evaluation of the finished product. We classified snow cover in this way from imagery collected during a lower snow cover year using drone imagery at Torgersen and Humble Islands on 14 and 15 January 2020 and a high snow cover year using satellite imagery from Geoeye-1 at both islands on 11 January 2019.

Penguin colonies

Adélie penguin nest sites group into spatially separated sub-colonies of various size and shape. Penguin sub-colony perimeters from Torgersen Island in 1998/99 were digitized in ArcGIS Pro 2.7.1 using a map from Patterson et al. (2003); we refer to these as “historic” perimeters. This map was aligned to a georeferenced image, and boundaries were traced around the colony perimeters. Using imagery from the January 2020 drone surveys, we outlined the perimeter of sub-colonies based on the extent of dark guano stains surrounding attended nests. In 2022, we walked the perimeter of Torgersen sub-colonies with a handheld GPS. We calculated the area of each sub-colony for all years. In cases where a large sub-colony fragmented into smaller sub-colonies in later years, we summed the smaller sub-colony areas.

Snow distribution models

Approach

We used two statistical modeling approaches to predict snow cover on Torgersen and Humble Islands in 2018–19 (more snow cover) and 2019–20 (less snow cover) (Fig. S2). We used two complementary, widely used, and well-established modeling approaches: generalized additive models (GAMs) and boosted regression trees (BRTs) (Elith et al. 2006; Oppel et al. 2012; Becker et al. 2020). Our first approach used GAMs to test which variables were most predictive of snow presence/absence by applying the information-theoretic model comparison framework to compare a suite of candidate models, evaluate multiple hypotheses, and select the most parsimonious set of best-approximating models using Akaike’s Information Criterion (AIC) (Johnson and Omland 2004; Stephens et al. 2005). To account for potential biases inherent in any single modeling approach, we then used BRTs to further evaluate a top performing GAM as BRTs are generally superior to other methods (Leathwick et al. 2006). We compared the results from the GAM and BRT with the same predictor variables to evaluate model performance and then used the best performing model to show spatial predictions of snow cover.

Generalized additive models

GAMs were used to test which variables were most predictive of the presence and absence of snow cover. We selected model variables to explore different representations of directional topography and to test whether hillshade explains snow cover better than aspect, represented as a circular variable, or its northness and eastness components. We created 10 candidate models for each island/year combination, including (1) solely directional topographic variables (aspect, northness and eastness, or hillshade) with five different azimuths tested for the hillshade-only models (350, 0, 10, 20, and 30°); and (2) three full models with each directional topographic variable, slope, and elevation. As five azimuths were tested for hillshade-only models, we generated only one full model that included hillshade, which included the best-performing hillshade parameterization.

GAMs can fit complex nonlinear relationships using a smoothness parameter estimated by generalized cross-validation using the R “mgcv” package. Models were run with a binomial error distribution. Because the presence-to-absence ratio of snow cover was skewed towards more absences, we randomly subsampled the absence data so that there was an equal number of presence and absence locations (Barbet-Massin et al. 2012). Aspect, as a circular variable, was modeled using a cyclic spline. The predictor variables within our candidate models were not collinear (TOR Pearson’s $R < 0.22$; HUM $R < 0.31$). All hillshade variables were highly correlated with each other (TOR $R > 0.76$; HUM $R > 0.82$) and each was positively correlated to northness (TOR $R > 0.67$; HUM $R > 0.75$). Of the 10 candidate models, the best fit models were identified using AIC, which allows for the determination of the most parsimonious model that accounts for the most variation with the fewest terms (Burnham and Anderson 2002). We reported the results of all tested models, including the R^2, the percentage of deviance explained, and Akaike weight (Table S1).

Boosted regression trees

The results from the GAMs informed our second modeling approach. The best GAMs with the lowest AIC include slope, elevation and either hillshade or aspect (Table S1). However, all full GAMs for each island/year group had nearly identical R^2 and deviance explained values. Given the similar performance, we used northness and eastness in our secondary BRT modeling approach. The reason was twofold: hillshade requires parameterization and is more difficult to interpret, and aspect is a circular variable complicating its inclusion in a regression framework. As with the GAMS, we used BRTs to model the presence/absence of snow on each island/year combination, separately.

BRTs can outperform other regression-based approaches, elucidate complex non-linear relationships, and handle missing data, outliers, multicollinearity, irrelevant predictors, and violations of traditional statistical assumptions (De'ath 2007; Elith et al. 2008). BRTs combine classification trees and include stochasticity to decrease model variance and improve predictive performance. We followed established protocols for fitting BRTs and used the 'brt.functions' package in R (Leathwick et al. 2006; Elith et al. 2008). Models were built using a bernoulli family, a tree complexity of 3, bag fraction of 0.6, and a learning rate such that at least 1000 trees were included in the model. Model results were evaluated using a set of diagnostic metrics: the relative influence of predictor variables, partial dependence plots, percentage of deviance explained, area under the receiver operating characteristic curve (AUC) and True Skill Statistic (TSS). AUC discriminates between true-positive and false-positive rates, and ranges from 0 to 1 where values > 0.5 indicates better than a random test (Hanley and McNeil 1982).

The BRT results were compared to the GAMs for independent model evaluation. Given similar but slightly better model performance, we used the BRTs to predict each model spatially onto the landscape data for each respective island/year. We ran 10 iterations of four-fold cross-validation where 75% of the data was used for training and 25% for testing, and we reported the mean and standard deviation in diagnostic metrics of the 10 model outputs.

Influence of island geomorphology on penguin sub-colony locations

We investigated the influence of island geomorphology derived from drone surveys on Adélie penguin occupation and extinction on Torgersen Island. First, we compared landscape variables (northness, eastness, slope, and elevation) within and outside of historic sub-colony perimeters to understand if penguins selected for specific features on the island. We used a Mann–Whitney U Test to determine significant differences between means as the data was not normally distributed. Second, we compared these variables within extinct (historic perimeters) and active sub-colonies (including, historic and 2022 perimeters) to understand if certain features created more suitable habitat to sustain breeding populations during the monitoring period. For active sub-colonies that fragmented as the population declined, we took an area weighted mean of the landscape variables per sub-colony. Using an analysis of variance (ANOVA) followed by a multiple comparison test using Tukey's Honest Significant Difference, we determined if the means differed between the three groups: within historic perimeters for extinct sub-colonies, historic perimeters for active sub-colonies, and 2022 perimeters for active sub-colonies.

Penguin demographic data and analyses

Near Palmer Station, the number of active nests (or breeding pairs) of Adélie penguins have been periodically censused since 1975, with annual monitoring beginning in 1991 (Supplemental Information S3). Colony censuses were performed in accordance with standardized methods (CCAMLR 1992) during peak egg-laying (mid-November). Using these census estimates, we calculated the percentage of the local breeding population that was active on Torgersen Island in 1975 and 2022. For extinct sub-colonies on Torgersen Island, we calculated the year of extinction (the first year when the number of active nests equaled zero) and if possible, population decline rates from 1991, and if not, 1993. Decline rates were only calculated for sub-colonies with more than two data points. Sub-colony decline rates were normalized by subtracting the mean and dividing by the standard deviation so that the data had a mean of 0 and standard deviation of 1. We used linear regression to test for a relationship between decline rate and extinction year using all data points and separately for north and south aspects, and calculated Pearson's correlation coefficients between colony area, extinction year and decline rate using all data points and separately for north and south aspects. For the analyses using decline rate or extinction year, we excluded an outlier with the fastest decline rate as this small sub-colony located on the north aspect was potentially negatively impacted by physiological research in 1995 and 1996 (Patterson 2001). We tested if mean historic sub-colony areas were significantly different between active and extinct sub-colonies as larger sub-colonies could take longer to reach extinction, and between extinct sub-colonies on north and south aspects using Welch's two sample t-test as specific habitats may support larger sub-colonies.

To estimate when active sub-colonies may become extinct, we calculated the number of years to extinction for similarly sized extinct colonies, which was defined as a population within 5% of the 2022 census. We calculated the mean and standard deviation for the number of years to extinction for north and south aspects, and we used these means to summarize the potential year range.

To understand Adélie penguin chick health at the end of the breeding season, we used a time series of annual mean chick fledging mass from 1991 to 2022 (Cimino et al. 2014) (no data was collected in 2021, Supplemental Information S3). We compared the mean annual chick fledging mass with the number of snow events during the breeding season to determine if chicks weighed less after snowy seasons. We tested for significant differences in snow events between years of lighter (< 3035 g, the non-survivor threshold) and heavier chicks (> 3035 g) using a t-test.

Results

Torgersen and Humble Island landscapes

Torgersen and Humble Islands are located in close proximity (< 1 km) but vary in their island geomorphology. Torgersen is circular (~ 300 m in diameter), gently sloped, and has one 18 m peak in the north-central part of the island (Fig. S3). It has a low-elevation, southwest-northeast ridge that divides the island into roughly north and south aspects. Humble Island has more complex features with separate high elevation peaks (~ 15 m) that are connected by regions of both flat and steep topography of varying aspects (Fig. S3).

Landscape features appear to create spatially variable patterns in snow deposition and accumulation. On Torgersen Island, satellite imagery showed typically the island was snow covered in the early spring (September) and nearly snow-free by late summer (February) (Fig. 2). The region that was snow-free first was the north aspect where active penguin sub-colonies are located. Satellite imagery showed complete snow melt on the island in some years, while in others, snow patches persisted, particularly in regions with a southern aspect and lower hillshade value (Fig. 2, S3).

Weather patterns

Snow accumulates during the winter (day 115 to 267, Fig. S4a), reaching a maximum snow depth typically in the spring (mean = 96.4 cm, range = 25–172 cm, Fig. S4b, c). Snow begins melting until the ground is snow-free in late spring to the early summer (Fig. S4d), and the timing of when the ground was snow-free has become later over time (Table S3). The first day with zero snow on the ground was correlated to both the day of the snow maximum ($R = 0.33$, $p = 0.057$) and depth of the snow maximum ($R = 0.60$, $p = 0.00025$). The average length of the snow accumulation, ablation and snow-free period were ~ 149, ~ 77 and ~ 140 days, respectively (Fig. S5abc). There was interannual variability in the frequency of snowy days, ranging from zero to 99 days, and an increase in the number of breeding season snow accumulation events over time, ranging from zero to 15 days (Fig. 3a, Table S3).

There were seasonal patterns in wind speed, where wind speeds were generally lowest in summer, and highest in winter and spring (Fig. S6). During the snow accumulation period each year, the number of 'windy days' ranged from zero to 32 days. We found a statistically significant decrease in the spring u wind component (i.e., more easterly winds over time) and increase in the winter v wind component (i.e., weaker northerly winds over time) (Table S3, Fig. S6).

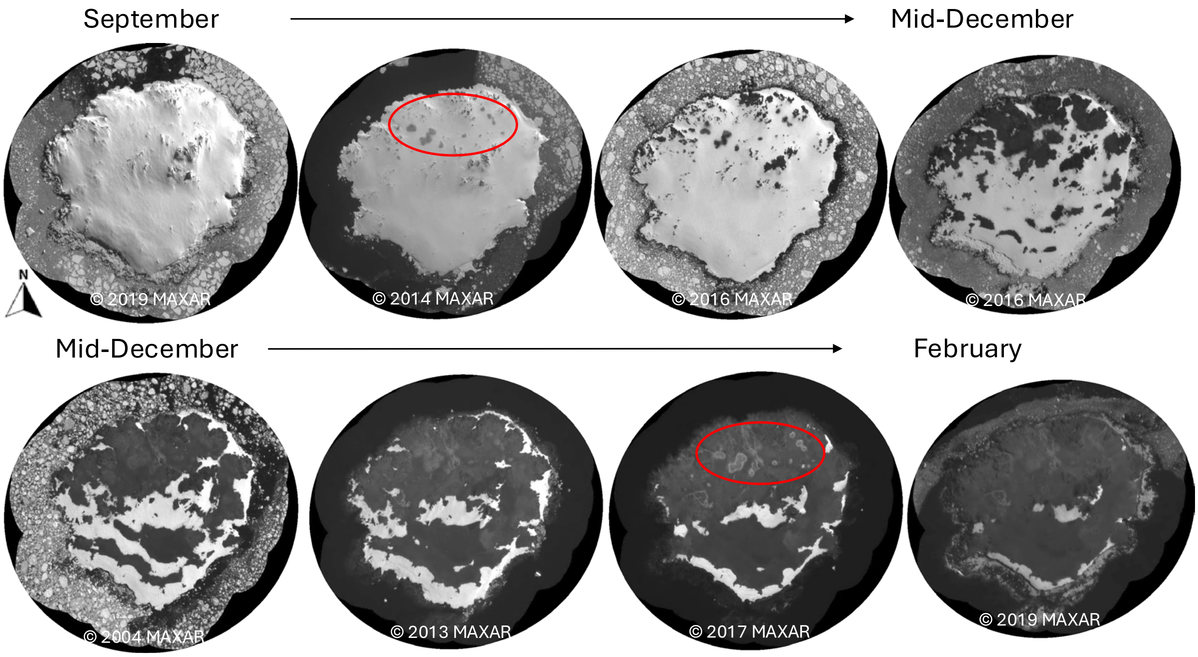

Fig. 2 The progression of snow cover on Torgersen Island from mostly snow covered in the early spring to nearly devoid of snow towards the end of summer. This spatial melt pattern was consistent across years, but the timing of melt varied. Penguins arrive in October, lay eggs in mid-November ideally as bare rock is exposed, and chicks hatch in mid-December as larger patches of bare rock are available. Active Adélie penguin colonies (within red circles) can be seen from October (second image) onwards with variable visibility due to image quality and contrast. The dates of each image from top left to bottom right: 2019-09-29, 2014-10-29, 2016-11-08, 2016-12-16, 2004-12-15, 2013-12-28, 2017-01-18, 2019-02-28 (Copyright Maxar, Table S2)

There were decadal patterns in snowy and windy years, where the frequency of snowy years decreased from four out of five years between 1990 and 1994 to zero between 2005 and 2009 (Fig. 3b). The trend reversed after 2009, and nearly each year since 2014 has been characterized as a snowy year (Fig. 3b). Analysis of the mean proportion of windy days showed a similar pattern (Fig. 3c). During less snowy years from 2000 to 2009, the proportions of windy days were low. Afterwards, the frequency of snowy years and the proportion of windy days increased.

Predictions of snow cover patterns

For the GAMs describing the presence/absence of snow, the best hillshade models were parameterized with wind directions of 0 or 350° (i.e., a northern direction), although the R^2 and deviance explained was often similar between most directional topography models (i.e., hillshade, aspect, and northness/eastness-only) within each island/year group (Table S1). The full models (including elevation, slope and a directional topographic variable) performed better than directional topography-only models. While a top full model was apparent using AIC comparisons, the R^2 and deviance explained was essentially the same for all full models within island/year groups. For these GAMs, Torgersen models had higher explained deviance than Humble by ~ 10–20%, and models for both islands had a higher explained deviance in 2019 (33% and 57%) than 2018 (17% and 26%) (Table S1).

The BRT models performed well in terms of deviance explained (23–72%), AUC (0.80–0.97) and TSS (0.44–0.86) (Table 1). Like the GAMs, BRT models of Torgersen snow cover performed better than those of Humble Island, and BRT models of 2019 (low snow cover) performed better than those of 2018 (high snow cover). As shown in other studies, the deviance explained was higher for BRTs than GAMs (Brodie et al. 2020).

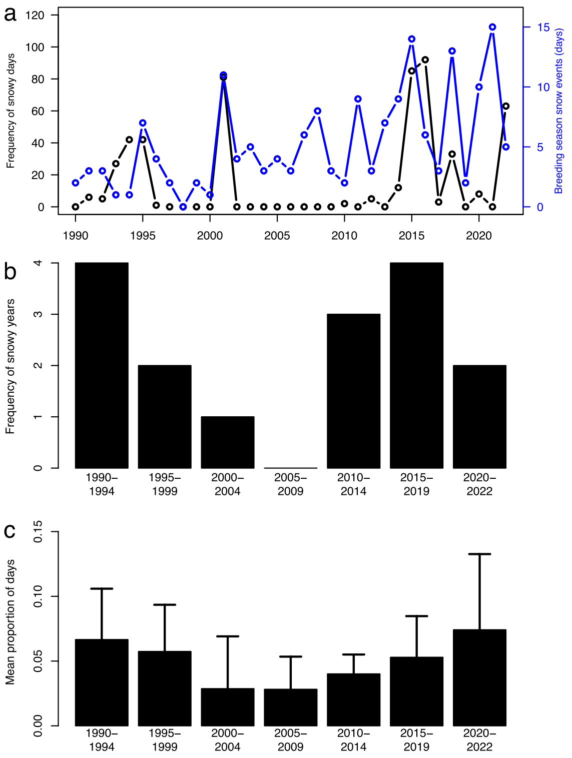

Fig. 3 Variability in snowy and windy years. **a** Frequency of days with snow depth $>$ 91 cm during the snow accumulation period at Palmer Station from 1990 to 2022 (black) and the number of days with snow accumulation ($\geq$ 1-cm) during the breeding season (blue). **b** The frequency of snowy years (max snow depth $>$ 91 cm). **b** Mean and standard deviation in the proportion of windy days (wind speed $>$ 13.3 m/s) during each year's snow accumulation period. **b** and **c** All bins include five years except for the last three-year bin

The model response curves showed similar patterns between different islands/years and modeling approaches. For Torgersen and Humble hillshade GAMs in both years, a lower hillshade value (or southerly aspect) corresponded to a higher probability of snow presence (Fig. S7). For GAM and BRT full models, snow was more likely to be present on flatter slopes, southerly aspects and low to intermediate elevations (Fig. S8-12). The variable percent contributions from BRTs showed elevation was the most important variable (~40–64%), in general followed by northness (~13–44%), slope (11–18%) and eastness (5–9%, Table 1).

Spatial predictions from the BRT models for each island/year provided further visual confirmation of model performance. Higher probability of snow cover was generally within the black contours where snow was observed (Fig. 4). This further highlighted the southerly and low-lying regions where snow was likely to be deposited and accumulated.

Sub-colony characteristics at Torgersen Island

Torgersen Island contained 59% of the local Palmer Station breeding population in 1975 (8988 of 15202 breeding pairs, Fraser et al. 1997), and 52% in 2022 (620 of 1197 breeding pairs), with only 7% of the 1975 Torgersen population active in 2022 (Fig. S13). In 1989, there were 23 active Adélie penguin sub-colonies (Patterson et al. 2003) on the west, north, and east regions of the island with an absence of colonies in the south during the observation period (Fig. 5a). Historic penguin sub-colonies were located at significantly higher elevations, and on more northerly and flatter slopes compared to regions outside of sub-colony perimeters ($p < 0.05$, Fig. S14).

By 2022, there were 18 extinct sub-colonies on Torgersen Island (south aspect $n = 10$, north aspect $n = 8$) and only five active sub-colonies on the north aspect, albeit some of the larger sub-colonies have fragmented into multiple smaller ones but remain within the footprint of the historic sub-colony perimeter (Fig. 5a). In 1993, there were 2237 breeding pairs on the south aspect and 5018 on the north aspect. By 2022, sub-colonies on the south aspect had decreased by 100%, while those on the north aspect had decreased by 88%. The extinct sub-colonies occupied an average area of 1578 m^2 (range: 212 to 3433 m^2) (Fig. 5b). Of the five active colonies, three had the largest historic area on the island (i.e., in 1998/99), with an overall mean of 4928 m^2 (range: 1462 to 8427 m^2), which was marginally significantly higher than the historic area of extinct sub-colonies (t-test, $t = -2.48$, $p = 0.06$). The 2022 active sub-colonies were small (mean area = 97 m^2, range: 24 to 275 m^2), containing between 15 and 396 breeding pairs (6–40% of the 1993 sub-colony populations) (Table 2, Fig. 5b, S13).

There were no significant differences between mean northness, eastness, slope and elevation within extinct and active sub-colony perimeters ($p > 0.05$, Fig. SS15). However, recognizing the small sample size of active sub-colonies, we note some extinct sub-colonies occupied regions with lower elevations and steeper slopes than active colonies in 2022. The

Table 1 Boosted regression trees were used to model snow presence/absence for two islands in two years

Snow model	AUC	% Dev. Expl	TSS	% Contribution Northness	% Contribution Eastness	% Contribution Elevation	% Contribution Slope
Torgersen Island 2018	0.88 ± 0.001	0.38 ± 0.01	0.60 ± 0.01	28.46 ± 0.47	9.37 ± 0.59	50.08 ± 0.46	12.09 ± 0.38
Torgersen Island 2019	0.97 ± 0.001	0.72 ± 0.001	0.86 ± 0.01	33.12 ± 0.5	4.56 ± 0.34	44.81 ± 0.9	17.51 ± 0.78
Humble Island 2018	0.80 ± 0.001	0.23 ± 0.01	0.44 ± 0.01	12.94 ± 0.41	6.79 ± 0.21	63.78 ± 0.53	16.49 ± 0.29
Humble Island 2019	0.90 ± 0.001	0.42 ± 0.01	0.65 ± 0.01	44.33 ± 0.76	5.15 ± 0.8	39.41 ± 0.98	11.1 ± 0.62

Area under the receiver operating characteristic curve (AUC), percent deviance explained (Dev.Expl), true skill statistic (TSS) and variable percent contribution. Numbers reported are the mean and standard deviation for 10 iterations of fourfold cross-validation

most prominent pattern was that extinct colonies occupied both south and north aspects while active colonies were only present on the north aspect. The 2022 active sub-colonies had a lower mean northness but higher mean elevation than historic sub-colonies (Fig. S15).

Focusing on extinct sub-colonies, there were relationships between sub-colony area, aspect, and decline rate. The historic areas of extinct sub-colonies on the north aspects (mean = 1203 m^2) were marginally smaller than sub-colonies on south aspects (mean = 1890 m^2) (t-test, $t = -1.86$, $p = 0.08$). On both north and south aspects, larger sub-colonies went extinct later than smaller colonies ($R = 0.75$, $p = 0.0009$), but sub-colonies on south aspects went extinct earlier than similarly sized sub-colonies on north aspects (Fig. 5c). On the south aspect, larger sub-colonies declined faster than smaller sub-colonies ($R = -0.84$, $p = 0.004$), but the relationship between decline rate and area was not significant on the north aspect ($p > 0.05$). The sub-colony with the steepest decline rate, declining by 51% from 1995 to 1996 (72 to 37 breeding pairs) went extinct in 2002, which was 3 and 11 years earlier than sub-colonies with a similar number of breeding pairs on south and north aspects, respectively.

We estimated extinction years for active sub-colonies based on the time to extinction for similarly sized sub-colonies on north- and south-facing slopes. While sample sizes were small, many sub-colonies on south aspects went extinct earlier than those on north aspects with a similar population (Table 2). For sub-colonies with < 30 breeding pairs, extinction may occur in 3 to 6 years (2025–2028). For sub-colonies with 80 to 100 breeding pairs, extinction may occur in 8 to 15 years (2030–2037). For sub-colonies with ~ 400 breeding pairs, our one example suggests extinction may occur in 25 years (2047).

Storm effects on penguin chicks

We tested if the number of snow events during the breeding season related to mean chick fledging mass. We found that during years with more snow events, the mean chick fledging mass was often below the threshold of non-survivors (t-test, $t = 1.90$, $p = 0.07$, Fig. 6) but chicks also fledged at a weight < 3035 g during breeding seasons with no snow events. However, in almost all years of high chick mass, there were very few snow events (median = 3).

Discussion

Penguins are sensitive indicators of the environment and food web, and their occupation history provides a window into past changes. As the rate of climate change and frequency of climate anomalies increase, understanding the mechanisms behind species population declines and extinctions is

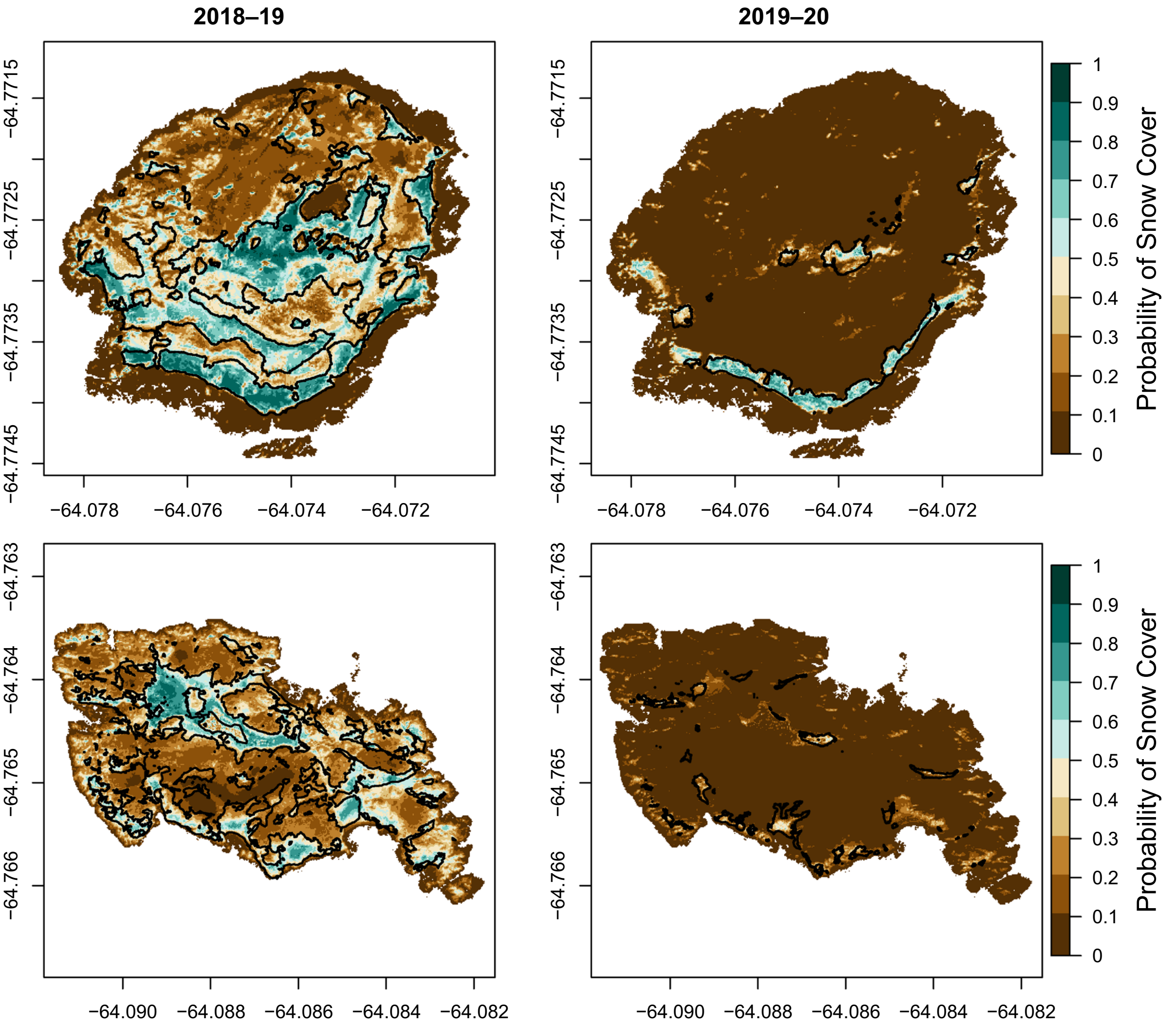

Fig. 4 Model output of the probability of snow cover. (Top) Torgersen and (bottom) Humble Islands in 2018 (i.e., January 2019, high snow cover) and 2019 (i.e., January 2020, low snow cover). The black lines are polygons of snow cover from imagery (Fig. S2) and mostly encompass regions of higher probability of snow cover

paramount. The questions we addressed here were challenging due to the inconsistent availability of some data sources. However, by using disparate datasets, we obtained a synoptic view of weather patterns and trends, the impacts of wind and landscape features on snow cover, and how this relates to penguin sub-colony extinction. Understanding the cascading effects of shifting weather patterns on habitat conditions and offspring health is crucial for anticipating the potential impacts of climate-induced changes on predators inhabiting Antarctic terrestrial ecosystems.

Long-term weather patterns and consequences for Adélie penguins

Paleoclimate records (Mulvaney et al. 2012), weather data since the 1950/70 s (Turner et al. 2005; Ducklow et al. 2006; Yu et al. 2020) and sea ice records during the satellite era (Simmonds and Li 2021) demonstrate the AP has warmed. Warming trends have been observed through permafrost thaw, glacial retreat, increased air temperature, and reduced sea ice near Palmer Station (Bockheim et al. 2013; Cimino et al. 2023b; Schofield et al. 2024). To detect these

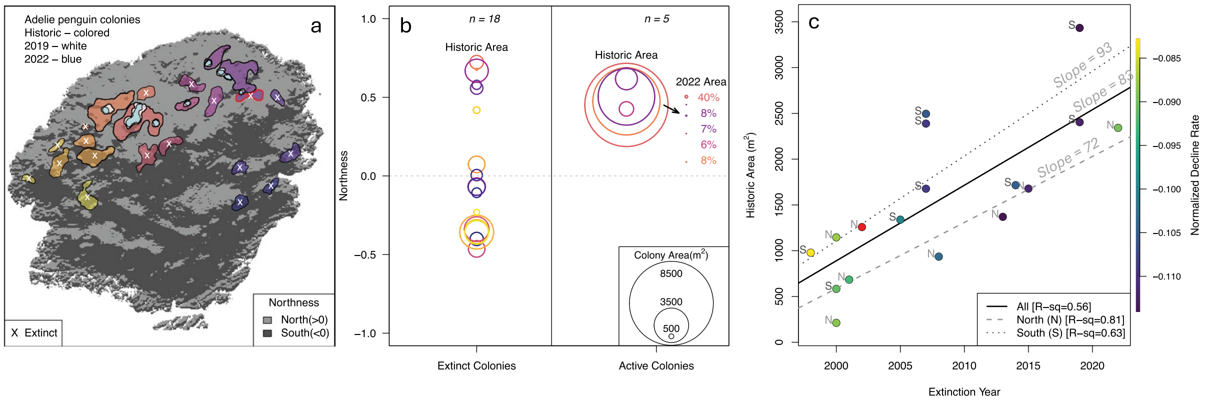

Fig. 5 Distribution and attributes of extinct and active Adélie penguin sub-colonies on Torgersen Island. **a** Colored, white, and blue polygons are larger historic, and smaller 2019 and 2022 sub-colonies. Extinct sub-colonies are marked with an 'x'. The island is colored by northness (north- or south-facing slope). **b** Extinct sub-colonies were on north and south aspects while active sub-colonies were only on north aspects. Colors correspond to sub-colony polygons in **a**. The size of the circle represents the colony area, historically or in 2022. The percentage of active nests in 2022 compared to 1993 is shown (earliest census data available). **c** For extinct sub-colonies, the historic area, decline rate and extinction year are shown. North (N) and south (S) represent the mean sub-colony northness. The linear relationships between area and extinction year were significant ($p<0.05$) with the R-squared and slope shown. The red point was not included in the regression as it was an outlier with a high decline rate (− 0.20), likely impacted by physiological research, and corresponds to the red outlined sub-colony in **a**

Table 2 The number of nests, colony area, and estimated number of years to extinction for active Adélie penguin sub-colonies in 2022

# of Nests in 1993	# of Nests in 2022 (% of 1993)	Historic/2022 sub-colony Area (m^2)	Years to extinction on north slopes	Years to extinction on south slopes	North/South mean extinction year
953	80 (8%)	5733/92	7.5 ± 4.9 (n = 2)	10.3 ± 6.8 (n = 3)	2030/2032
397	29 (7%)	2218/34	6 (n = 1)	6 ± 2.8 (n = 2)	2028/2028
254	15 (6%)	1462/24	5 (n = 1)	2.8 ± 1 (n = 4)	2027/2025
999	396 (40%)	8427/275	NA (n = 0)	25 (n = 1)	NA/2047
1271	100 (8%)	6804/60	14.5 ± 0.7 (n = 2)	8 ± 2.8 (n = 2)	2037/2030

A similarly sized colony was defined as a population within 5% of the 2022 census. The mean, standard deviation, and sample size (n) are reported

The percentage of active nests in 2022 compared to 1993 is also shown in Fig. 4. Number of years to extinction for similarly sized extinct colonies on the north- and south-facing slopes was determined. The mean extinction year is based on the mean number of years to extinction for each slope aspect

changes, long time series are often required due to the high interannual variability in the Antarctic (Zhang et al. 2019; Fogt et al. 2022). During our study period, despite the backdrop of multidecadal warming, there were few significant trends in wind and snow properties from 1990 to 2022. However, we detected decadal periods of windy and snowy conditions. At other AP research stations, increased air temperature and precipitation were observed from the ~ 1970s to 2020, but there were similar decadal patterns with a warmer/high precipitation period to the late/early 1990s, a cooler/low precipitation period to the mid/early-2010s, and then another warmer/high precipitation period afterwards (Carrasco and Cordero 2020; Carrasco et al. 2021).

One significant trend was the snow-free period starting later, beginning in early November in the early 1990s and late December in the early 2020s. This could be related to the decreasing trend in the spring u wind component, where colder easterly

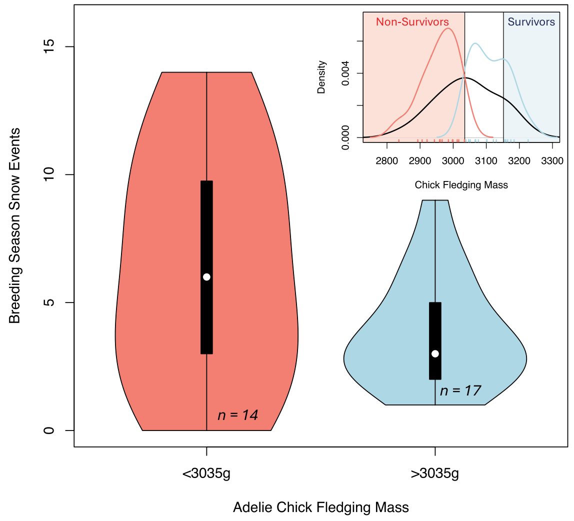

Fig. 6 Chick mass in relation to snow events. Probability density of the number of snow events during the breeding season between annual mean Adélie penguin chick fledging masses above and below the threshold mass of non-surviving chicks (3035 g). Thick black vertical lines are the interquartile range, thinner black lines are the upper and lower adjacent values, and white points are the median. The smaller subplot shows the density and values of annual mean chick fledging mass above (blue line) and below the threshold for non-surviving chicks (red line), and all chick masses (black line). The threshold for surviving chicks is > 3152 g (blue shaded area, n = 6)

winds in recent years could be playing a role in delaying snow melt. Adélie penguins have a synchronous breeding phenology with a short temporal window to breed after returning from a winter migration (Fraser et al. 1992; Hinke et al. 2012). At Torgersen and Humble Islands, Adélie penguins adjust their breeding phenology with spring sea ice and snow conditions leading to interannual differences ranging from a few days to a week (Cimino et al. 2019), not weeks to months over which their environment varies, making them vulnerable to environmental mismatches (Cimino et al. 2023a). The average clutch initiation date (November 15) coincided with when the ground was historically snow-free, but recently, snow-free terrain occurs about one month later near the timing of chick hatch (December 20, Cimino et al. 2019). This suggests at least a periodic misalignment of the average 5-month snow-free period (now beginning in December) with the 5-month Adélie penguin breeding season (October–February) as the decadal trends in the length of the snow-free season (ranging from ~ 3 to > 6 months) appear to match snowy/windy periods (Fig. S5). The consequences of deep snow at the timing of clutch initiation include deferred breeding, egg or chick death through the flooding or wetting of nests, and delayed phenology leading to reduced breeding success (Massom et al. 2006; Youngflesh et al. 2017), and a later start to the snow-free season has been related to lower chick fledging mass (Cimino et al. 2023a).

We also detected more snow events during the penguin breeding season, with generally < 5 events per breeding season from the 1990s to 2005 and up to ~ 10–15 events after 2015. As chicks age, their ability to thermoregulate increases, but the wetting of chick down increases heat loss and reduces their ability to maintain their body temperature (Taylor 1985). The metabolic costs of wetting can be further amplified by high winds. Therefore, these increased thermoregulatory costs could result in a lower body mass at fledging and reduced overwinter survival (Chappell et al. 1990; Chapman et al. 2010, 2011). In agreement with past work at Humble Island (Chapman et al. 2010, 2011; Cimino et al. 2014, 2023a), we found a negative impact of precipitation, specifically more snow events related to lower chick fledging mass.

Landscape features drive snow cover patterns

Snow accumulation and cover varied spatially as evidenced by the snow stake data, and drone and satellite imagery. The occurrence of uneven snow accumulation across a heterogeneous landscape is well documented in the literature but this is the first study to show this spatial pattern on fine scales near Palmer Station. By developing statistical models to predict snow cover distribution at local scales, we determined topographic factors that influenced the spatial variability in snow dynamics. Elevation contributed the most to model performance as snow accumulates more in low lying areas than at high elevations. Northness was the second most important factor, following the hypothesis that snow accumulates disproportionately on landscapes with a southern exposure where the dominant north-northeast winds shift snow loads from north- to south-facing slopes (Fraser and Patterson 1997). Other studies using statistical models have also shown similar factors, often elevation, slope and an aspect-type variable, were good predictors of snow distribution (Grünewald et al. 2013).

In our modeling framework, we tested many directional topographic variables to obtain the most parsimonious and interpretable explanation. While models that included hillshade, aspect, or northness/eastness had nearly identical model performance and provided the same mechanistic relationships, AIC ranking suggested the inclusion of hillshade often resulted in the "best" full model. AIC is designed to penalize unnecessary complexity to find a balance between fit and simplicity. Models including northness and eastness were slightly more complex (4 vs. 3 terms), and without improving model fit, resulted in a higher AIC value despite having the easiest values to interpret. We acknowledge aspect and hillshade models were adequate but conclude that models with parameterized derived variables can be more complex to interpret and thus, not always preferred.

We found that models performed better in low snow years and for Torgersen Island. High snow cover resulted in snow on a wider range of landscape features, despite having varying snow depths, which led to a less predictive model. In comparison, during a low snow year, snow was present on a narrow range of features that facilitate accumulation and retention. The landscape of Humble Island is more complex and difficult to model than Torgersen, as it has many small ridges and valleys that complicate how terrain features drive snow melt and deposition. Future work could apply more complex numerical snow accumulation or evolution models (Liston and Elder 2006; Schneiderbauer and Prokop 2011; Vionnet et al. 2012; Groot Zwaaftink et al. 2013) that include topography and meteorological data, and processes such as melt, sublimation, deposition, saltation, energy balance, and erosion.

Landscape-driven penguin occupation and extinction

Both Humble and Torgersen Island are important breeding sites for Adélie penguins in the Palmer Station area. Penguin occupations began ~ 500 cal yr BP (Emslie 2001) with colonized locations likely related to the availability of bare rock and nesting pebbles in the early spring, resulting in penguins selecting nesting habitats at higher elevations or in areas that accumulate less snow and become snow-free first. Higher elevations were also related to higher Adélie penguin sub-colony quality in the Ross Sea (Schmidt et al. 2021).

The extinction of sub-colonies appears to be related to geomorphology, as all sub-colonies on the south aspect went extinct on Torgersen Island. Additionally, the extinct sub-colonies on the north aspect took longer to disappear than similarly sized ones on the south aspect, supporting that more suitable breeding habitats exist on the north aspect. Other Palmer Station studies have found that landscape-driven snow impacts were greater on some islands than others (Cimino et al. 2019) and that islands with more suboptimal (southwest aspect) habitat have faster population declines (Fraser et al. 2013).

The paleoecological record provides further support for the influence of landscape-driven nest microclimate on penguin colony locations. On Ardley Island in the northern AP, *Pygoscelis* penguin colonies moved locations from one side of the island to another during the last millennium due to a change in wind direction, wind scour, and snow accumulation modulated by topography (Yang et al. 2019). More recently, snow accumulation and wind exposure explained spatial variability in Adélie penguin population trends in East Antarctica (Bricher et al. 2008), spatial terrain features associated with snowdrift risk were related to breeding success in the Ross Sea and Pointe Géologie Archipelago (Schmidt et al. 2021; Méheust et al. 2024), and vanishing snow patches along with glacier retreat allowed for colony expansion in the Ross Sea (LaRue et al. 2013). While modern and past penguin responses suggest that microclimate plays a role in regulating population trends and colony locations, responses may vary regionally due to site-specific differences in weather or terrain.

Other mechanisms

Being a species that nests on land, forages at sea and undergoes a winter migration, there are many factors required for Adélie penguin survival. Chicks fledging at a low weight in non-snowy years also supports this. Adélie penguin foraging behavior and prey characteristics vary, including type, quality, and availability (Fraser and Hofmann 2003; Saba et al. 2014; Pickett et al. 2018; Ainley et al. 2018). This variability combined with the southward contraction and reduced biomass of their main prey, Antarctic krill (*Euphausia superba*), should be considered (Kawaguchi et al. 2024). Building large nests reduces the impact of moisture and snow (McLatchie et al. 2024), and consuming high-quality prey can compensate for the effects of extreme chick wetting (Chapman et al. 2011). Small, isolated sub-colonies with a low perimeter-to-area ratio may experience increased predation by skuas (Schmidt et al. 2021), where proximity to skua nests may drive breeding success over landscape features (Méheust et al. 2024). Winter sea ice conditions impact Adélie penguin behavior and survival (Ballerini et al. 2009; Jongsomjit et al. 2024), which may be amplified by the recent anomalous sea ice lows (Purich and Doddridge 2023). Compound effects of multiple suboptimal conditions may also be at play. With the greater appreciation of landscape and snow effects, a focused multiparameter analysis could disentangle how various drivers interact.

Conclusion

Adélie penguins are largely in decline throughout the west AP, which is often attributed to warming trends, reduced sea ice and changes in prey (Trivelpiece et al. 2011; Cimino et al. 2016; Wethington et al. 2023). However, apart from these widely accepted control factors, we add to the emerging views demonstrating the importance of non-marine variables. Understanding the drivers of penguin populations can inform management efforts as the goals of the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) include conserving marine life, promoting sustainable resource use, and ensuring ecosystem-based management considers species needs. Our results also have implications for other penguin population trends in the Antarctic and beyond that are subject to increasing precipitation or periodic high precipitation years. Our approach is transferable and scalable to other regions where satellite imagery, satellite/drone-derived digital elevation models, and statistical or machine learning approaches could be used to understand snow cover and species distribution patterns over larger scales. Snow cover dynamics are an often overlooked yet important feature of bird occurrence and abundance but are rarely used to understand bird distributions (Keyser et al. 2023). There is no time like the present to collect data on snow and landscape conditions relative to species distributions, especially as weather patterns change and these sensitive bioindicators of our climate continue to disappear.

Acknowledgements We are grateful for the efforts of many technicians that contributed to the long-term penguin monitoring, and we especially thank Bill Fraser and Donna Patterson-Fraser who led this research for many decades and developed the initial hypotheses tested here. We thank the Palmer Station Research Associates who maintained the weather data, including Lance Roth, Marissa Goerke, Evan Quinter, and Ben Rosen-Filardo, and those who participated in drone surveys and data processing, including Rebecca Edgell.

Author contributions MAC and DVG conceived of the study. MAC collected some of the penguin data and GDL conducted drone surveys with support and oversight from DWJ. GDL processed the raw drone data, DVG processed the weather data, and MAC conducted all other analyses. MAC wrote the paper with significant contributions from GDL and DVG. All authors approved of the final manuscript.

Funding Geospatial support for this work was provided by the Polar Geospatial Center under National Science Foundation Office of Polar Programs (NSF-OPP) awards 1043681 and 1559691. Funding was also provided by NSF-OPP awards 2012444, 2026045, 2012247 and 2012365.

Data availability Satellite images were requested and acquired from the Polar Geospatial Center. Datasets are available from the Environmental Data Initiative at: https://pallter.marine.rutgers.edu/catalog/edi/index.php, specifically, weather data (Palmer Station Antarctica LTER and Information Manager 2019) are available at: https://doi.org/https://doi.org/10.6073/pasta/cddd3985350334b876cd7d6d1a5bc7bf; penguin chick fledging mass data (Palmer Station Antarctica LTER et al. 2022a) are available at: https://doi.org/https://doi.org/10.6073/pasta/875086ecf38755f29f7aa8209e839e7f; and penguin census data (Palmer Station Antarctica LTER et al. 2022b) are available at: https://doi.org/https://doi.org/10.6073/pasta/805f6b97593c60cfdfd02266db9ab4b6. Drone survey data are available from the Duke Research Data Repository (Larsen et al. 2022): https://doi.org/https://doi.org/10.7924/r4sf2xs2w.

Declarations

Competing interests The authors declare no competing interests.

References

Ainley DG, Dugger KM, La Mesa M et al (2018) Post-fledging survival of Adélie penguins at multiple colonies: chicks raised on fish do well. Mar Ecol Prog Ser 601:239–251

Ananicheva M, Callaghan TV, Dahl-Jensen D, et al (2011) Snow, water, ice and permafrost in the Arctic (SWIPA): climate change and the cryosphere. Arctic Monitoring and Assessment Programme (AMAP)

Ballerini T, Tavecchia G, Olmastroni S et al (2009) Nonlinear effects of winter sea ice on the survival probabilities of Adélie penguins. Oecologia 161:253–265

Barbet-Massin M, Jiguet F, Albert CH, Thuiller W (2012) Selecting pseudo-absences for species distribution models: how, where and how many? Methods Ecol Evol 3:327–338

Becker EA, Carretta JV, Forney KA, Barlow J, Brodie S, Hoopes R, Jacox MG, Maxwell SM, Redfern JV, Sisson NB, Welch H (2020) Performance evaluation of cetacean species distribution models developed using generalized additive models and boosted regression trees. Ecol Evol 10:5759–5784

Bockheim J, Vieira G, Ramos M et al (2013) Climate warming and permafrost dynamics in the Antarctic Peninsula region. Glob Planet Change 100:215–223

Bricher PK, Lucieer A, Woehler EJ (2008) Population trends of Adélie penguin (Pygoscelis adeliae) breeding colonies: a spatial analysis of the effects of snow accumulation and human activities. Polar Biol 31:1397–1407

Brodie SJ, Thorson JT, Carroll G et al (2020) Trade-offs in covariate selection for species distribution models: a methodological comparison. Ecography 43:11–24

Burnham D, Anderson K (2002) Model selection and multimodel inference: a practical information-theoretic approach Springer-Verlag. NY USA, New York

Carrasco JF, Cordero RR (2020) Analyzing precipitation changes in the northern tip of the Antarctic peninsula during the 1970–2019 period. Atmosphere 11:1270

Carrasco JF, Bozkurt D, Cordero RR (2021) A review of the observed air temperature in the Antarctic Peninsula. Did the warming trend come back after the early 21st hiatus? Polar Sci 28:100653

CCAMLR (1992) CCAMLR ecosystem monitoring program (CEMP). Standard methods for monitoring studies. Scientific Committee for teh Conservation of Antarctic Living Marine Resources. Hobart, Australia

Chapman EW, Hofmann EE, Patterson DL, Fraser WR (2010) The effects of variability in Antarctic krill (Euphausia superba) spawning behavior and sex/maturity stage distribution on Adélie penguin (*Pygoscelis adeliae*) chick growth: a modeling study. Deep Sea Res Part II Top Stud Oceanogr 57:543–558

Chapman EW, Hofmann EE, Patterson DL et al (2011) Marine and terrestrial factors affecting Adélie penguin Pygoscelis adeliae chick growth and recruitment off the western Antarctic Peninsula. Mar Ecol Prog Ser 436:273–289

Chappell MA, Morgan KR, Bucher TL (1990) Weather, microclimate, and energy costs of thermoregulation for breeding Adélie Penguins. Oecologia 83:420–426

Chown SL, Convey P (2016) Antarctic entomology. Annu Rev Entomol 61:119–137

Cimino MA, Fraser WR, Patterson-Fraser DL et al (2014) Large-scale climate and local weather drive interannual variability in Adélie penguin chick fledging mass. Mar Ecol Prog Ser 513:253–268

Cimino MA, Lynch HJ, Saba VS, Oliver MJ (2016) Projected asymmetric response of Adélie penguins to Antarctic climate change. Sci Rep 6:28785

Cimino MA, Patterson-Fraser DL, Stammerjohn S, Fraser WR (2019) The interaction between island geomorphology and environmental parameters drives Adélie penguin breeding phenology on neighboring islands near Palmer Station, Antarctica. Ecol Evol 9:9334–9349

Cimino MA, Conroy JA, Connors E et al (2023a) Long-term patterns in ecosystem phenology near Palmer Station, Antarctica, from the perspective of the Adélie penguin. Ecosphere 14:e4417

Cimino MA, Goerke MA, Bent S (2023b) Sixty years of glacial retreat behind Palmer Station, Antarctica. Antarct Sci 35:415–417

Convey P, Chown SL, Clarke A et al (2014) The spatial structure of Antarctic biodiversity. Ecol Monogr 84:203–244

Dadic R, Mott R, Lehning M, Burlando P (2010) Wind influence on snow depth distribution and accumulation over glaciers. J Geophys Res Earth Surf 115:2009JF001261

Dattler ME, Lenaerts JTM, Medley B (2019) Significant spatial variability in radar-derived West Antarctic accumulation linked to surface winds and topography. Geophys Res Lett 46:13126–13134

De'ath G (2007) Boosted trees for ecological modeling and prediction. Ecology 88:243–251

Descamps S, Hudson S, Sulich J et al (2023) Extreme snowstorms lead to large-scale seabird breeding failures in Antarctica. Curr Biol 33:R176–R177

Ducklow HW, Baker K, Martinson DG et al (2006) Marine pelagic ecosystems: the West Antarctic Peninsula. Philos Trans R Soc B Biol Sci 362:67–94

Eayrs C, Li X, Raphael MN, Holland DM (2021) Rapid decline in Antarctic sea ice in recent years hints at future change. Nat Geosci 14:460–464

Elith JH, Graham CP, Anderson R, Dudík M, Ferrier S, Guisan AJ, Hijmans R, Huettmann FR, Leathwick J, Lehmann A, Li J (2006) Novel methods improve prediction of species' distributions from occurrence data. Ecography 29:129–151

Elith J, Leathwick JR, Hastie T (2008) A working guide to boosted regression trees. J Anim Ecol 77:802–813

Emslie SD (2001) Radiocarbon dates from abandoned penguin colonies in the Antarctic Peninsula region. Antarct Sci 13:289–295

Favero-Longo SE, Worland MR, Convey P et al (2012) Primary succession of lichen and bryophyte communities following glacial recession on Signy Island, South Orkney Islands, Maritime Antarctic. Antarct Sci 24:323–336

Fogt RL, Sleinkofer AM, Raphael MN, Handcock MS (2022) A regime shift in seasonal total Antarctic sea ice extent in the twentieth century. Nat Clim Change 12:54–62

Fraser WR, Hofmann EE (2003) A predator^{1}s perspective on causal links between climate change, physical forcing and ecosystem response. Mar Ecol Prog Ser 265:1–15

Fraser WR, Patterson DL (1997) Human disturbance and long-term changes in Adélie penguin populations: a natural experiment at Palmer Station, Antarctic Peninsula. In: Battaglia B, Valencia J, Walton DWH (eds) Antarctic communities: species, structure and survival, scientific committee for Antarctic research (SCAR), sixth biological symposium. Cambridge University Press, New York

Fraser WR, Trivelpiece WZ, Ainley DG, Trivelpiece SG (1992) Increases in Antarctic penguin populations: reduced competition with whales or a loss of sea ice due to environmental warming? Polar Biol. https://doi.org/10.1007/BF00237945

Fraser WR, Patterson-Fraser DL, Ribic CA et al (2013) A non-marine source of variability in Adélie penguin demography. Oceanography 26:207–209

Groot Zwaaftink CD, Cagnati A, Crepaz A et al (2013) Event-driven deposition of snow on the Antarctic Plateau: analyzing field measurements with SNOWPACK. Cryosphere 7:333–347

Grünewald T, Stötter J, Pomeroy JW et al (2013) Statistical modelling of the snow depth distribution in open alpine terrain. Hydrol Earth Syst Sci 17:3005–3021

Hanley JA, McNeil BJ (1982) The meaning and use of the area under a receiver operating characteristic (ROC) curve. Radiology 143:29–36

Hinke JT, Polito MJ, Reiss CS et al (2012) Flexible reproductive timing can buffer reproductive success of Pygoscelis spp. penguins in the Antarctic Peninsula region. Mar Ecol Prog Ser 454:91–104

Johnson JB, Omland KS (2004) Model selection in ecology and evolution. Trends Ecol Evol 19:101–108

Jongsomjit D, Lescroël A, Schmidt AE et al (2024) Going with the floe: Sea-ice movement affects distance and destination during A délie penguin winter movements. Ecology 105:e4196

Kawaguchi S, Atkinson A, Bahlburg D et al (2024) Climate change impacts on Antarctic krill behaviour and population dynamics. Nat Rev Earth Environ 5:43–58

Keyser SR, Fink D, Gudex-Cross D et al (2023) Snow cover dynamics: an overlooked yet important feature of winter bird occurrence and abundance across the United States. Ecography 2023:e06378

Kim SC, Kim JS, Hong BR et al (2016) Assembly processes of moss and lichen community with snow melting at the coastal region of the Barton Peninsula, maritime Antarctic. J Ecol Environ 40:8

Larsen GD, Varga HF, Patterson-Fraser DL et al (2024) Drone-based monitoring and geomorphology of southern giant petrel nests near Palmer Station, western Antarctic Peninsula. Polar Biol 47:459–474

Larsen GD, Falvo C, Tuohy C, et al (2022) Aerial data from drone surveys of coastal habitats on the West Antarctic Peninsula during austral summer (January–March 2020 and February–March 2019)

LaRue MA, Ainley DG, Swanson M et al (2013) Climate change winners: receding ice fields facilitate colony expansion and altered dynamics in an Adélie penguin metapopulation. PLoS ONE 8:e60568

Leathwick JR, Elith J, Francis MP et al (2006) Variation in demersal fish species richness in the oceans surrounding New Zealand: an analysis using boosted regression trees. Mar Ecol Prog Ser 321:267–281

Lindsay JB (2016) Whitebox GAT: A case study in geomorphometric analysis. Comput Geosci 95:75–84

Liston GE, Elder K (2006) A distributed snow-evolution modeling system (SnowModel). J Hydrometeorol 7:1259–1276

Liston GE, Sturm M (1998) A snow-transport model for complex terrain. J Glaciol 44:498–516

Marks D, Winstral A (2001) Comparison of snow deposition, the snow cover energy balance, and snowmelt at two sites in a semiarid mountain basin. J Hydrometeorol 2:213–227

Massom RA, Stammerjohn SE, Smith RC et al (2006) Extreme anomalous atmospheric circulation in the West Antarctic Peninsula region in austral spring and summer 2001/02, and its profound impact on sea ice and biota. J Clim 19:3544–3571

McCrystall MR, Stroeve J, Serreze M et al (2021) New climate models reveal faster and larger increases in Arctic precipitation than previously projected. Nat Commun 12:6765

McDonald BI, Goebel ME, Crocker DE, Costa DP (2012) Biological and environmental drivers of energy allocation in a dependent mammal, the Antarctic fur seal pup. Physiol Biochem Zool 85:134–147

McLatchie MJ, Emmerson L, Wotherspoon S, Southwell C (2024) Delay in Adélie penguin nest occupation restricts parental investment in nest construction and reduces reproductive output. Ecol Evol 14:e10988

Méheust Y, Delord K, Bonnet-Lebrun A-S et al (2024) Human infrastructures correspond to higher Adélie penguin breeding success and growth rate. Oecologia 204:675–688

Mulvaney R, Abram NJ, Hindmarsh RCA et al (2012) Recent Antarctic Peninsula warming relative to Holocene climate and ice-shelf history. Nature 489:141–144

Nex F, Remondino F (2014) UAV for 3D mapping applications: a review. Appl Geomat 6:1–15

Oppel S, Meirinho A, Ramírez I, Gardner B, O'Connell AF, Miller PI, Louzao M (2012) Comparison of five modelling techniques to predict the spatial distribution and abundance of seabirds. Biol Conserv 156:94–104

Palmer Station Antarctica LTER, Information Manager P (2019) Daily averaged weather timeseries (air temperature, pressure, wind speed, wind direction, precipitation, sky cover) at Palmer Station, Antarctica combining manual observations (1989 - Dec 12, 2003) and PALMOS automatic weather station measurements (Dec 13, 2003 - March 2019).

Palmer Station Antarctica LTER, Cimino M, Fraser W (2022a) Adelie penguin chick fledging weights, 1991–2021

Palmer Station Antarctica LTER, Cimino MA, Fraser WR (2022b) Adelie penguin area-wide breeding population census, 1991–2021 ver 8. Environmental Data Initiative

Patterson DL, Easter-Pilcher A, Fraser WR (2003) The effects of human activity and environmental variability on long-term changes in Adelie penguin populations at Palmer Station, Antarctica. In: Huiskes AHL, Gieskes WWC, Rozema J, Schorno RML, van der Vies SM, Wolff WJ (eds) Antarctic biology in a global context. Backuys Publishers, Leiden

Patterson DL (2001) The effects of human activity and environmental variability on long-term changes in Adélie penguin populations at Palmer Station, Antarctica. PhD Thesis, Montana State University-Bozeman, College of Letters & Science

Pearson LE, Weitzner EL, Tomanek L, Liwanag HE (2022) Metabolic cost of thermoregulation decreases after the molt in developing Weddell seal pups. J Exp Biol 225:242773

Pickett EP, Fraser WR, Patterson-Fraser DL et al (2018) Spatial niche partitioning may promote coexistence of *Pygoscelis* penguins as climate-induced sympatry occurs. Ecol Evol 8:9764–9778

Pomeroy JW, Marsh P, Gray DM (1997) Application of a distributed blowing snow model to the Arctic. Hydrol Process 11:1451–1464

Post E, Forchhammer MC, Bret-Harte MS et al (2009) Ecological dynamics across the arctic associated with recent climate change. Science 325:1355–1358

Purich A, Doddridge EW (2023) Record low Antarctic sea ice coverage indicates a new sea ice state. Commun Earth Environ 4:314

R Core Team (2022) R: A language and environment for statistical computing

Radok U (1977) Snow drift. J Glaciol 19:123–139

Ropert-Coudert Y, Kato A, Meyer X et al (2015) A complete breeding failure in an Adélie penguin colony correlates with unusual and extreme environmental events. Ecography 38:111–113

Saba GK, Fraser WR, Saba VS et al (2014) Winter and spring controls on the summer food web of the coastal West Antarctic Peninsula. Nat Commun 5:4318. https://doi.org/10.1038/ncomms5318

Schmidt AE, Ballard G, Lescroël A et al (2021) The influence of subcolony-scale nesting habitat on the reproductive success of Adélie penguins. Sci Rep 11:15380

Schneiderbauer S, Prokop A (2011) The atmospheric snow-transport model: SnowDrift3D. J Glaciol 57:526–542

Schofield O, Cimino M, Doney S, Friedlaender A, Meredith M, Moffat C, Stammerjohn S, Van Mooy B, Steinberg D (2024) Antarctic pelagic ecosystems on a warming planet. Trends Ecol Evol 39:1141–1153

Simmonds I, Li M (2021) Trends and variability in polar sea ice, global atmospheric circulations, and baroclinicity. Ann NY Acad Sci 1504:167–186

Stephens PA, Buskirk SW, Hayward GD, Martinez Del Rio C (2005) Information theory and hypothesis testing: a call for pluralism. J App Ecol 42(4):v12

Taylor JRE (1985) Ontogeny of thermoregulation and energy metabolism in pygoscelid penguin chicks. J Comp Physiol B 155:615–627

Tewari K, Mishra SK, Salunke P, Dewan A (2022) Future projections of temperature and precipitation for Antarctica. Environ Res Lett 17:014029

Thomas ER, Marshall GJ, McConnell JR (2008) A doubling in snow accumulation in the western Antarctic Peninsula since 1850. Geophys Res Lett 35:1–5

Thomas ER, Van Wessem JM, Roberts J et al (2017) Regional Antarctic snow accumulation over the past 1000 years. Clim past 13:1491–1513

Trew BT, Maclean IMD (2021) Vulnerability of global biodiversity hotspots to climate change. Glob Ecol Biogeogr 30:768–783

Trivelpiece WZ, Hinke JT, Miller AK et al (2011) Variability in krill biomass links harvesting and climate warming to penguin population changes in Antarctica. Proc Natl Acad Sci 108:7625–7628

Turner J, Lachlan-Cope T, Colwell S, Marshall GJ (2005) A positive trend in western Antarctic Peninsula precipitation over the last 50 years reflecting regional and Antarctic-wide atmospheric circulation changes. Ann Glaciol 41:85–91

van de Pol M, Jenouvrier S, Cornelissen JHC, Visser ME (2017) Behavioural, ecological and evolutionary responses to extreme climatic events: challenges and directions. Philos Trans R Soc B Biol Sci 372:20160134

Van Lipzig NPM, King JC, Lachlan-Cope TA, Van Den Broeke MR (2004) Precipitation, sublimation, and snow drift in the Antarctic Peninsula region from a regional atmospheric model. J Geophys Res Atmospheres 109:2004

Vionnet V, Brun E, Morin S et al (2012) The detailed snowpack scheme crocus and its implementation in SURFEX v7.2. Geosci Model Dev 5:773–791

Westoby MJ, Brasington J, Glasser NF et al (2012) 'Structure-from-Motion' photogrammetry: a low-cost, effective tool for geoscience applications. Geomorphology 179:300–314

Wethington M, Flynn C, Borowicz A, Lynch HJ (2023) Adélie penguins north and east of the 'Adélie gap'continue to thrive in the face of dramatic declines elsewhere in the Antarctic Peninsula region. Sci Rep 13:2525

World Meteorology Organization (2023) Guidelines on the definition and characterization of extreme weather and climate events. Switzerland, Geneva

Wu Q, Brown A (2022) whitebox:"WhiteboxTools" R frontend. R Package Version 2:

Yang L, Gao Y, Sun L, Xie Z, Yang W, Chu Z, Wang Y, Xu Q (2019) Enhanced westerlies drove penguin movement at 1000 yr BP on Ardley Island, west Antarctic Peninsula. Quat Sci Rev 214:44-53

Youngflesh C, Jenouvrier S, Li Y et al (2017) Circumpolar analysis of the Adélie Penguin reveals the importance of environmental variability in phenological mismatch. Ecology 98:940–951

Yu L, Zhong S, Sun B (2020) The climatology and trend of surface wind speed over Antarctica and the Southern Ocean and the implication to wind energy application. Atmosphere 11:108

Zhang L, Delworth TL, Cooke W, Yang X (2019) Natural variability of Southern Ocean convection as a driver of observed climate trends. Nat Clim Change 9:59–65