

GENTOO PENGUIN *PYGOSCELIS PAPUA* OCCUPATION AND COLONIZATION IN RELATION TO GLACIAL RETREAT AND SEA ICE DECLINE NEAR PALMER STATION, ANTARCTICA

MEGAN A. CIMINO^{1*}, PIERCE KIM², GREGORY LARSEN³, WILLIAM FRASER⁴, DAVID W. JOHNSTON³,
DONNA PATTERSON-FRASER⁴, DARREN ROBERTS¹, & MEGAN ROBERTS¹

¹*Institute of Marine Sciences, University of California Santa Cruz, Santa Cruz, California, United States* *(mecimino@ucsc.edu)

²*The College of Liberal Arts and Sciences, Biological Sciences, Arizona State University, Tempe, Arizona, United States*

³*Division of Marine Science and Conservation, Nicholas School of the Environment, Duke University Marine Laboratory, Beaufort, North Carolina, United States*

⁴*Polar Oceans Research Group, Sheridan, Montana, United States*

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ABSTRACT

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As glaciers retreat in Antarctica, ice-free areas create new opportunities for seabird colonization and range expansion. Highly mobile species, such as seabirds, can rapidly take advantage of these opportunities by establishing new colonies, but it remains unclear how quickly they can respond and what habitats they prefer. The Gentoo Penguin *Pygoscelis papua* is one species considered to be a climate change winner, as their populations have increased and they have expanded their range southward amidst rapid climate change along the western coast of the Antarctic Peninsula. Here, we provide a case study at Point 8, Anvers Island, involving satellite-based documentation of glacial retreat, drone-based habitat mapping, and the monitoring of Gentoo Penguin occupation as they colonize newly exposed land. Gentoo Penguins were first observed at Point 8 in the winter of 2019, which coincided with rapid glacial retreat between 2018 and 2020. They nested first in 2020 but did not successfully rear chicks until 2023, following low sea ice years. We hypothesize that Gentoos arrived here as juveniles and began nesting at 2–4 years of age, upon reaching maturity, but did not successfully breed until the age of 5–6 years. The increase in the number of molting adults suggests continuous immigration has been occurring. The time between glacial loss and colonization may suggest the colonization process can happen more quickly than previously thought. Continued sea ice decline and glacial retreat may support further range expansion and colonization by Gentoo Penguins in the study region.

Key words: Gentoo Penguin, colonization, climate winner, glacial retreat, habitat selection

INTRODUCTION

Antarctica is experiencing accelerated warming, especially evident along the west Antarctic Peninsula (WAP). There, length of the sea ice season has declined, and air temperature has warmed, leading to recession of glaciers (Silva et al., 2020; Simmonds & Li, 2021; Yu et al., 2020), which in turn has resulted in seals, penguins, and plants expanding their ranges (Cannone et al., 2022; Convey & Hughes, 2023; Roland et al., 2024). In this context, pygoscelid penguin species can act as biological indicators (Durant et al., 2009): pagophilic Adelie Penguin *Pygoscelis adeliae* populations have declined, while ice-avoiding Gentoo Penguin *P. papua ellsworthi* populations have increased (Clucas et al., 2014; Herman et al., 2020). The sub-Antarctic-dwelling Gentoo Penguin appears to have weaker natal philopatry than is generally thought for penguins. It has expanded its range southward into the Antarctic Peninsula, contemporaneously with regional warming and high population growth (Clucas et al., 2014; Cole et al., 2019; Ducklow et al., 2007; Lynch et al., 2008, 2012). This success has been attributed to a flexible life history strategy, evident in aspects of the species' breeding, diet, and phenology (Bent et al., 2025; Black et al., 2018; Hinke et al., 2012; Lescroël et al., 2004; Pickett et al., 2018). As the range of Gentoo Penguins expands, it is unclear why

certain locations were chosen for new breeding colonies and how these colonies were established.

Near Palmer Station, penguin populations have been monitored periodically since the mid-1970s and annually since 1991, a period during which the sea ice season has dramatically declined (Fig. 1). The oldest Gentoo colony near Palmer Station is in the Joubin Islands, with nesting first documented in 1974 (Parmelee et al., 1977). In 1993, Gentoo Penguins established a new breeding colony at Biscoe Point at which subsequent rapid population growth was evident (Ducklow et al., 2007). The success of Gentoo Penguins contrasts with trends of the long-established Adelie Penguins at this site, which have declined > 90% since the mid-1970s (Emslie et al., 1998; Schofield et al., 2024; Smith et al., 1999).

This present case study examines the potential roles of glacial recession, sea ice, topographic elevation, and immigration in the southward range expansion of Gentoo Penguins. We hypothesized that colonization is dependent upon the availability of high-elevation rocky nesting habitats that allow earlier access to nesting pebbles, and low winter sea ice cover that facilitates access to the ocean for this non-pagophilic species. We measured glacial recession from satellite imagery and describe its timing in relation

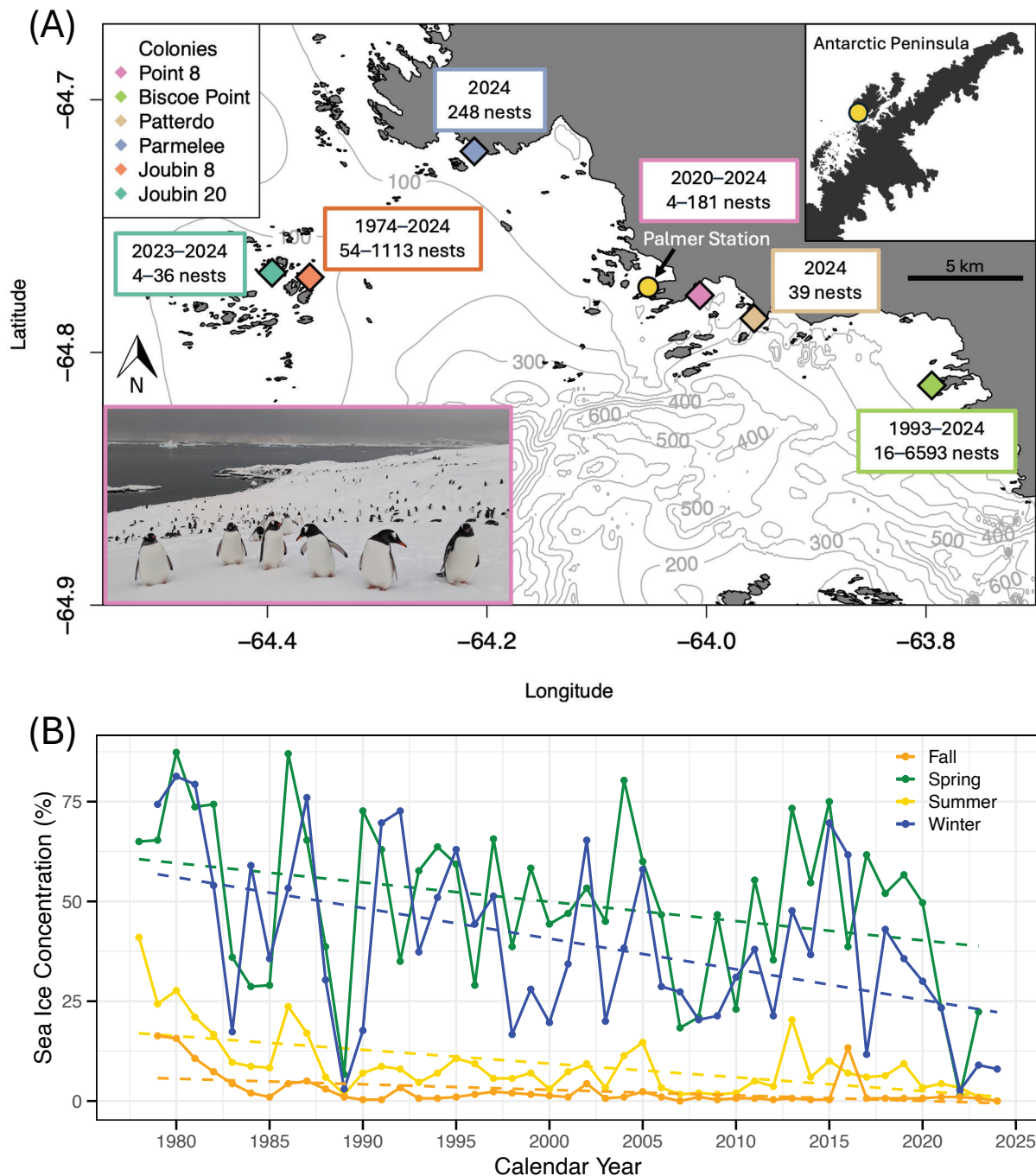


Fig. 1. (A) Map showing Palmer Station (yellow circle), located on Anvers Island, west Antarctic Peninsula (inset), and Gentoo Penguin *Pygoscelis papua* colonies (diamonds); photo from Point 8 (July 2020, photo credit: Ken Keenan). Dark areas show land masses. Bathymetry is indicated in units of meters. Colored boxes describe the period of Gentoo Penguin occupancy at each location and the number of active nests from the first observation (if available) and during the 2024 breeding season. (B) Average seasonal sea ice concentration near Anvers Island. Dashed lines are significant trends ($p < .05$).

to colonization. To evaluate whether Gentoo Penguins select higher elevations for nesting, we also used a drone-derived digital surface model (DSM) combined with Gentoo Penguin distribution and abundance monitored through conventional field observations. On the basis of these merged datasets, we document how immigration, estimated age and experience, increasing habitat availability, and nesting habitat preferences support Gentoo Penguin colonization in locations exposed by glacial retreat.

METHODS

Study Site and History

This study focuses on a region near Palmer Station, Anvers Island, along the WAP (64.77°S, 064.05°W) and is part of the Palmer Antarctica Long-Term Ecological Research (LTER) program. Anvers Island is a large (61 km long), mountainous island that is

mostly glaciated except for patchy coastal areas. Point 8 is located ~2.5 km east of Palmer Station (Fig. 1). The presence of penguins close to the station was a notable attraction for staff, especially as most wildlife leaves the area before winter. Penguin monitoring and drone-based surveys were carried out in accordance with the approved guidelines of the University of California, Santa Cruz, and Duke University Institutional Animal Care and Use Committee (UCSC code: Cimim2204dn).

Penguin Data

At Point 8, multiple aspects of penguin colony and population dynamics were monitored during breeding seasons of 2020–2024. Note that we refer to years using the first year in a split year; i.e., 2020 refers to the 2020/21 austral summer. Censuses were conducted to count active nests, adults, and chicks every five days or as weather allowed and were discontinued if all nests failed. In 2023 and 2024, we counted molting adults. Individual nest sites or colony perimeters were marked or circumambulated using a handheld GPS. Other natural history observations and species occurrences were occasionally noted to understand possible competition for space and potential predators (Appendix 1, available on the website). We also received anecdotal observations of Gentoo Penguin presence and approximate abundance from Palmer Station staff during periods of 2019–2024 when no seabird field biologists were at Palmer Station.

In the Palmer Station vicinity, Gentoo Penguins have colonized a few other islands that have not been reported elsewhere. We report the number of active nests from the first year of observation, if available, and for 2024 (Appendix 1).

Sea Ice Data

Average monthly sea ice concentration (SIC) during the period 1978–2024, within an area ~200 km by ~200 km off Anvers Island, was derived from data from NASA's Scanning Multichannel Microwave Radiometer (SMMR) and from Special Sensor Microwave/Imager (SSM/I) sensors on the US Defense Meteorological Satellite Program's satellites (Palmer Station Antarctica LTER & Stammerjohn, 2024). We computed seasonal averages and used linear regression to test for trends in sea ice over time to provide environmental context.

Satellite Imagery and Glacial Terminus Mapping

We obtained archival satellite images of the Point 8 region for 2004–2024, collected by QuickBird and WorldView satellites (Maxar, Westminster, Colorado) and provided by the Polar Geospatial Center. Optical and multispectral satellite scenes are often obscured by cloud cover in Antarctica, and low snow cover was necessary to delineate the glacial terminus, though some terminus estimates might still include adjacent snow. These preconditions limited the amount of useful imagery, so we visually filtered candidate imagery to a subset of 10 images (Table A1, Appendix 1) that occurred during summertime, after most snow cover melted.

We visually located the edge of the glacial terminus (i.e., the interface between glacial ice and bare rock) in georeferenced satellite imagery and manually traced this edge in ArcGIS Pro. For each image, we generated 200 random points along the line of the terminus edge and calculated, for each point, the nearest distance to the terminus edge in the chronologically preceding image from

our subset. This produced a set of 200 distance measurements for each image, describing the extent of terminus movement since the time of the previous image. Measurements at point locations that occurred within the glacial extent of the chronologically previous image were recorded as negative distances (recession) and measurements beyond the glacial extent of the previous image were positive distances (advancement). We calculated the mean and standard deviation of the recession distance for each year.

Drone-Derived Elevation Data

We used a previously processed DSM for Point 8 (Larsen et al., 2024, 2025), available from the Duke Research Data Repository (Larsen et al., 2022), with data collected on 30 January 2020 using a DJI Phantom 4 Pro drone with a default camera payload and produced using structure from motion photogrammetry using PIX4Dmapper. Drone data were collected under US Antarctic Conservation Act permit ACA 2020-016 and NOAA permit 14809-0. The DSM describes the elevation at 0.2-m ground sample distance in the EGM96 vertical datum. We used this DSM to determine the elevation of penguin sub-colonies and background habitat outside sub-colony perimeters, excluding the contemporaneous glacier extent and any terrain below −0.31 m (the highest high-tide line during 2018–2020), by extracting values for all cells in these regions. We evaluated whether penguins selected for higher-elevation nesting sites by comparing the elevation data within each sub-colony with the background data using a *t*-test and applied a Bonferroni correction to adjust *p* values for multiple comparisons. We determined significance using $\alpha = .05$ and ensured all statistical assumptions were met.

RESULTS

Glacial Retreat and Sea Ice Decline

Regarding available nesting habitat, we describe glacial retreat exposing ice-free land during the period from 1985 to 2022. From 1985 to 1999, Point 8 was glaciated (Landsat and USGS, Google Earth). In 2004, rock became exposed in the northeast region. Overall, annual retreat then averaged 50.72 m across the terminus during 2006–2023 (Fig. 2A), with a maximum retreat of 124.43 m in one section. However, initially, during 2006–2009, the glacier advanced on average 1.67 m/year, which was then followed by retreat: 5.91 m/year in 2009–2010, 0.75 m in 2010–2011, and 1.81 m in 2016–2017. A mean advancement of 0.74 m/year occurred in 2017–2018, and fastest recessions occurred in 2018–2020 (9.30 m/year) and 2020–2022 (6.17 m/year; Fig. A1 in Appendix 1).

From 1979 to 2024, SIC declined in winter ($p < .001$) and spring ($p = .03$). In the early years, SIC was often $> 50\%$ but by 2021–2024 was reduced to $< 25\%$ (Fig. 1B). SIC also declined during the fall ($p < .001$) and summer ($p < .001$), with concentrations at ~10%–20% in the early years and ~0%–10% in recent years.

Penguin Winter–Spring Occupation

During the winters of 2019 and 2020, hundreds of Gentoo Penguins were intermittently present at Point 8 (K. Bernard and K. Keenan, personal communication, 2020; Fig. 1). More specifically, in 2020, Gentoos were present in July, disappeared for parts of August, were present in late September, and gathered on snow-free ridges in October. In October–November 2021 and 2022 and September

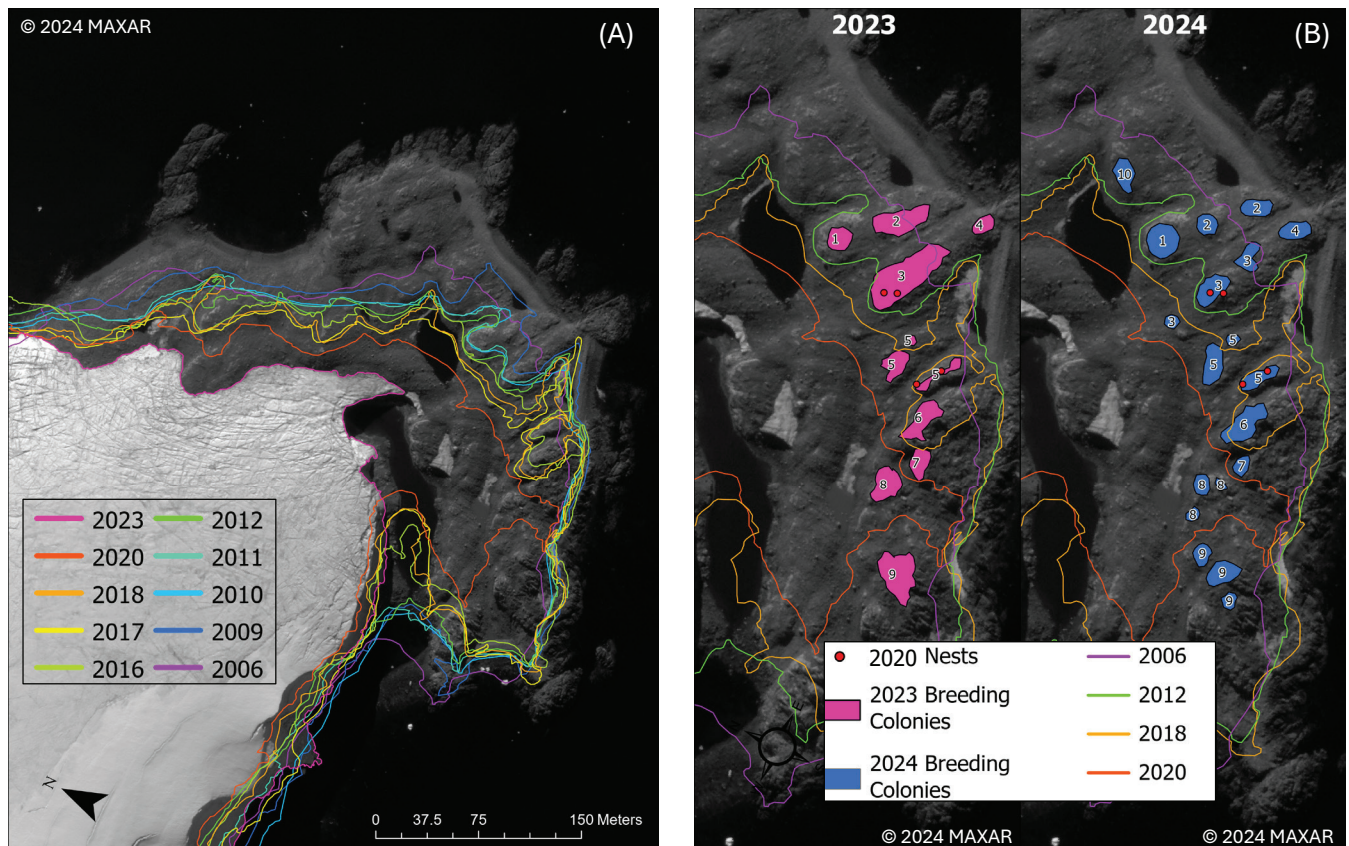


Fig. 2. Glacier extent and Gentoo Penguin *Pygoscelis papua* sub-colonies at Point 8. (A) The glacier terminus for years with suitable imagery. (B) A subset of glacier terminus lines along with nest sites (red points, 2020) and sub-colony perimeters (2023 in pink; 2024 in blue). One nest occurred in 2022 (not shown) within the area that would become sub-colony 9. In 2023, the sub-colonies were mapped earlier in the season and included non-nesting adults, yielding larger sub-colonies. In 2024, sub-colonies only encompassed active nests, yielding smaller, fragmented sub-colonies. Basemap in both (A) and (B) is true color imagery captured on 04 March 2024 (WorldView-3, ©2024 Maxar; Table A1, Appendix 1).

2022, 100–150 Gentoo Penguins were present in small numbers (J. Mossen and A. Klemmedson, personal communication, 2022). During 2023, at least 20–30 Gentoo Penguins appeared to be present all winter (K. Keenan, A. Tomita, R. Kaplan, personal communication, 2023). In July 2024, ~10–80 Gentoo Penguins were regularly present but were absent in August, potentially related to extensive local sea ice (S. Anderson, personal communication, 2024). In early September 2024, ~50 Gentoo Penguins were present, and by mid-October hundreds of Gentoo Penguins were regularly observed, as ridges became snow-free.

Penguin Colonization

On 08 December 2020, four nests with two eggs each were documented. Piles of small rocks suggested additional nest building. On 16 December, three nests were abandoned and six eggs depredated, presumably by nearby Brown Skuas *Stercorarius antarcticus*. On 04 January 2021, the one remaining nest was also abandoned. Gentoo Penguins remained present at least until June 2021 (H. James, personal communication, 2021). In 2021, nests were present, but neither eggs nor chicks were observed (M. Goerke, personal communication, 2021) in this year during which station construction prevented research. Gentoos were present at least until June 2022 (A. Klemmedson, personal communication,

2022). In 2022, we documented one active nest with at least one egg on 08 December, but it failed. More nest building was evident this year compared to the previous year, with most nests being of poor quality (small, containing few rocks).

On 23 November 2023 (peak egg-laying census), we documented nine sub-colonies with 1–16 active nests in each (total $n = 64$; Fig. 3A), and on 29 January (chick census), these sub-colonies had reared 33 chicks (Fig. 3B). For sub-colonies 1, 6, 7, and 9, the breeding success (number of chicks per number of nests) ranged from 0.56 to 0.93 chicks/pair (mean = 0.7). The presence of adults in sub-colonies decreased over time, though some adults remained to molt and rest post-molt in late March–April (Fig. 3C). The total number of adults within the sub-colonies fluctuated widely when counts occurred at different times of day; fewer adults were generally present midday. After 29 January, near the time of crèche formation, chicks left their sub-colonies and congregated mainly with adults along the shoreline. The number of chicks decreased slightly from January to late February, then more steeply to early March as they fledged (Fig. 3C). In early February, we noted a surprising abundance of molting adults and began monitoring counts, finding peaks in mid-late February (266) and late March–early April (177; Fig. 3C). Notably, the total number of molting penguins (443) far exceeded the number of breeding penguins (128 parents from 64 nests).

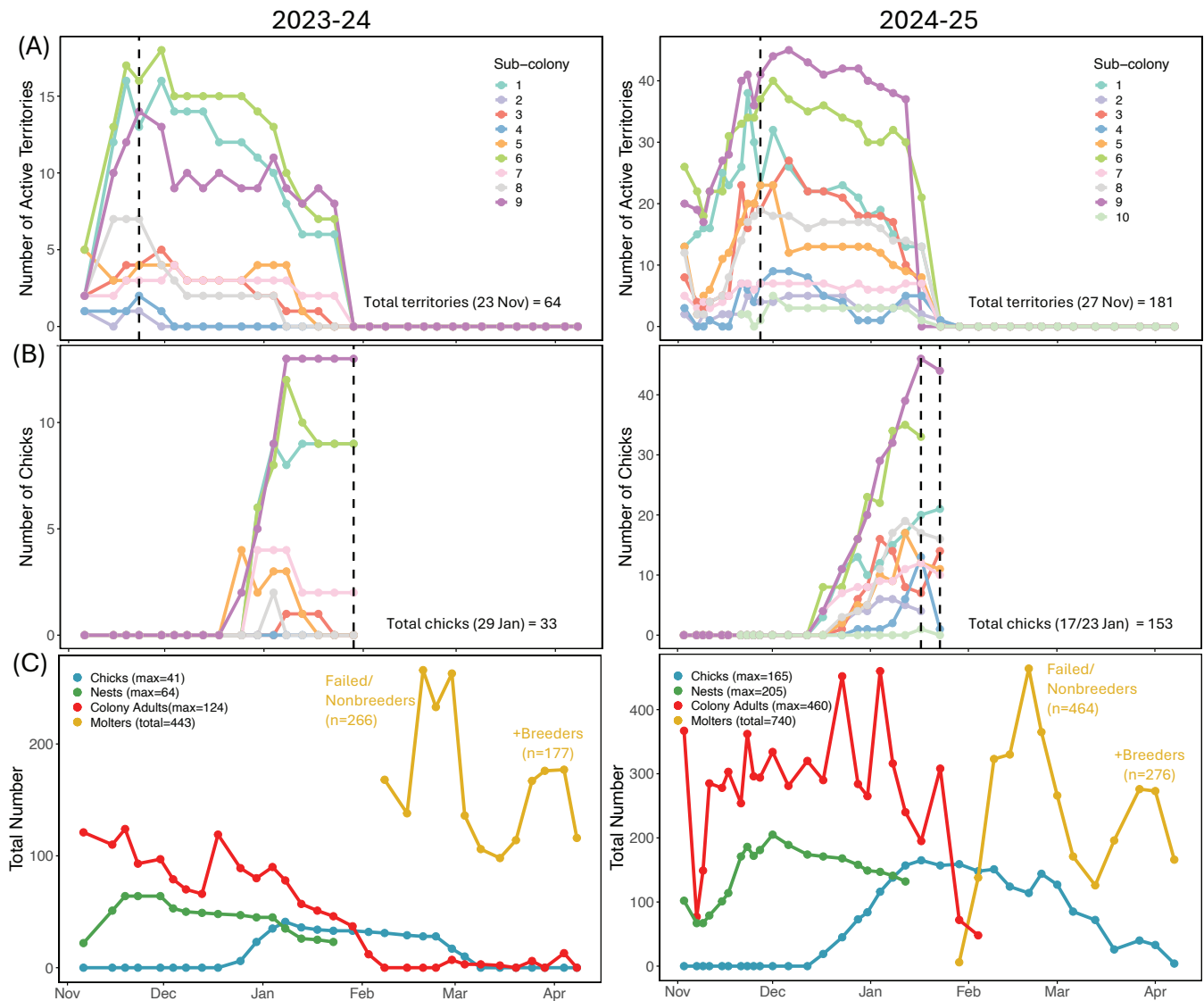


Fig. 3. Within-season monitoring of Gentoo penguins *Pygoscelis papua* at Point 8 during 2023–2024 (left) and 2024–2025 (right). (A) The number of active territories within each sub-colony; vertical dashed lines indicate the dates (23 November 2023 and 27 November 2024) of the active nest censuses. Individual nests cannot be distinguished, as chicks become more mobile and form crèches in late January. (B) The number of chicks within each sub-colony; vertical dashed lines indicate dates (29 January 2024 and 17/23 January 2025) of the chick censuses near the time of chick crèche formation. Chicks mixed between colonies or relocated to nearby regions, such as the beach, after the time in crèche. (C) The total number of chicks, active nests, and adults in sub-colonies, and the number of molting adults throughout the Point 8 region. Based on timing, we presume the first peak of molters includes failed or non-breeders and the second peak also includes breeders.

In 2024, peak egg-laying occurred on 27 November 2024, with a total of 181 nests (Fig. 3A). A maximum count of 205 nests occurred on 01 December, which likely included many adults sitting tight on a nest but not laying eggs (e.g., sub-colonies 1 and 3). Nesting rock piles were often abandoned and later reoccupied. The chick census used counts from two dates (17 and 23 January, $n = 153$) because chicks were mobile and mixed between some sub-colonies (Fig. 3B). The breeding success was 0.74–1.4 chicks per pair (mean = 0.87), excluding outlier sub-colonies 5 (0.5 chicks/pair) and 10 (0 chicks/pair). High counts of adults occurred in the late afternoon of 23 December and 04 January, then decreased through February (Fig. 3C). Due to time constraints, we stopped counting non-molting adults after early February but noted that some adults molted in sub-colonies or were present after completing molt

in late March–April. We also observed freshly molted penguins building nests and displaying courting behavior (year-round nest building occurs at northerly sites; Williams, 1990). We counted molting adults at the first observation on 29 January (Fig. 3C) and encountered peaks in mid-February (464) and late March (276). The number of molting penguins ($n = 740$) again exceeded the number of breeding penguins (410 parents).

The Influence of Elevation on Colonization

A satellite image from 16 December 2023 indicated that snow-free ridges were available during incubation (Fig. 4A). Unoccupied habitat had an elevation range of -0.28 to 23.81 m (mean = 7.14 m), and sub-colonies were located at a mean elevation of 8–10 m,

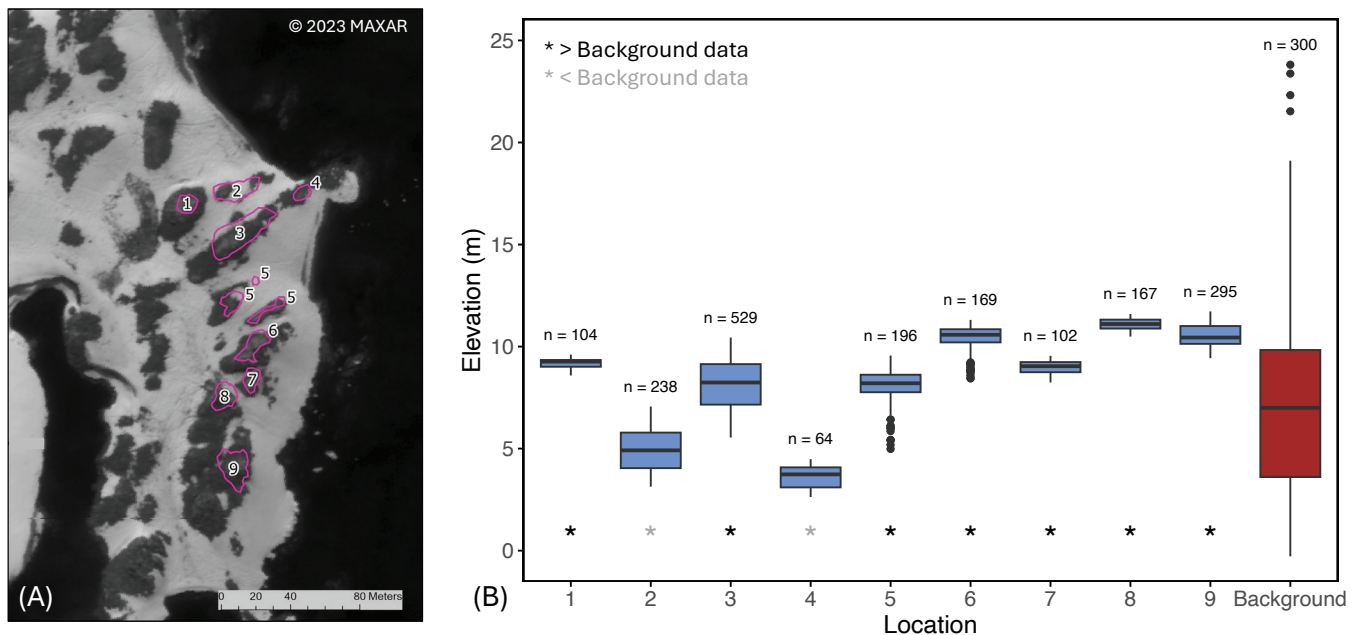


Fig. 4. Gentoo Penguin *Pygoscelis papua* sub-colony locations and corresponding elevation measurements. (A) Sub-colonies (pink) in 2023 overlaid on a 06 December 2023 satellite image (WorldView-3, ©2023 Maxar; Table A1, Appendix 1) during the incubation period, showing available snow-free nesting habitat on ridges. (B) Comparison of sub-colony elevation data (blue) and background terrain (brown) showing that most sub-colonies occurred at significantly higher elevations than the background (black asterisks), except for significantly lower sub-colonies 2 and 4 (gray asterisks). Number of cells in each boxplot is labeled (*n*).

except for sub-colonies 2 and 4 (3–5 m). Sub-colonies 2 and 4 were at a significantly lower mean elevation, while all other sub-colonies were at a significantly higher mean elevation than the background data (*t*-test, $p < .05$, Fig. 4B).

DISCUSSION

Overall, the presence of Gentoo Penguins near Palmer Station has escalated from being rare to being a daily occurrence in notable numbers in less than a decade. Gentoo Penguins established colonies at locations where Adelie Penguins currently or formerly nested (Joubins 8 and 20, Biscoe Point) or at recently deglaciated sites adjacent to Anvers Island (Parmelee, Patterdo, Point 8). The present case study from Point 8 sheds light on how colony establishment appears to occur, related to both glacial retreat and reduced winter sea ice cover. Glacier retreat is not unique to the vicinity of Palmer Station (Cimino et al., 2023), as 60% of the glaciers along the Antarctic Peninsula are retreating (Silva et al., 2020); ice-free areas are expected to expand in the future (Lee et al., 2017). Extrapolating from this localized study area to the broader WAP, there may have been a substantial increase in Gentoo colony establishments in recent years, although we acknowledge that invasion fronts are often patchy. Our findings characterize some of the habitats selected during colonization and contribute to a broader understanding of how this species may respond to climate change in the future.

Gentoo Penguin Occupation and Colonization

At Point 8, the largest measured glacier recession, from 2018 to 2020, coincided with sightings of hundreds of Gentoo Penguins during the winter/spring of 2019 and 2020, and the establishment of four nests in 2020. The second-largest measured recession, from 2020 to 2023, was followed by the establishment of nine sub-colonies in 2023 and

the first year of successful breeding. At Point 8 and in the wider study region, there was a large increase in active nests and chicks reared in 2023 and 2024 at multiple sites, perhaps also related to SIC lows from 2022 onward compared to historic conditions.

The phenology of Gentoo Penguins at Point 8 resembles other colonies within their southern range (Black et al., 2018; Fig. A2A, Appendix 1). The two peaks in molting adults (consistent with the ~20-day molt duration; Adams & Brown, 1990) may represent initial pulses of immature penguins, non-breeders, or failed breeders followed by a second wave of successful breeders, as in all pygoscelid species (Dodino et al., 2018; Penney, 1967; Trivelpiece & Trivelpiece, 2013). The greater number of molting penguins relative to breeding penguins indicates that colonization may follow molting at a site.

During winter, anecdotal observations showed tens to hundreds of Gentoo Penguins were often present at Point 8. In multiple years, Gentoo Penguin absence was possibly related to extensive local SIC that forced them to vacate the region for better access to open water in which to forage, as seen elsewhere (Black et al., 2017). In comparison, at sub-Antarctic colonies where there is no sea ice, Gentoo Penguins attend sites continuously through the winter (Dodino et al., 2018). Thus, low SIC may be an important driver of colonization and breeding success.

The onset of unsuccessful nesting after first observed presence, followed by the increase in nest-building activities annually, the abandonment and reoccupation of rock piles without egg laying, and then successful nesting (Fig. A2B, Appendix 1) may suggest that first breeders at Point 8 could be juvenile Gentoo Penguins engaged in practice nesting. Based on this timeline, we hypothesize that most Gentoo Penguins immigrated to Point 8 as juveniles

(Fig. A2C, Appendix 1). In the winter of 2019, ~6-month-old Gentoo Penguins may have arrived, with a few attempting to breed upon reaching 2 years of age in 2020. While Gentoos are capable of breeding at 2 years, most breed by the age of 3 or 4 (Williams, 1995; Williams & Rodwell, 1992). When successful breeding occurred in 2023, based on our hypothesis, this cohort of penguins would be nearly 5 years old. Penguins at Point 8 may not all be the same age, as we found evidence for additional immigration each year (i.e., more molters) rather than one immigration event.

Interpretation Considerations at Point 8

Gentoo Penguins may have been present during winters before 2019. One staff member indicated no penguins were present during the winters of 2015 and 2016 (L. Roth, personal communication, 2024), and if Gentoos were present in 2017 or 2018, it was likely in small numbers given the greater glacial extent and lack of suitable nesting habitat, as ridges were covered by ice (Fig. 2B).

The nest censuses in November 2023 and 2024 may have overestimated the number of active nests in some sub-colonies. Fewer active nests were counted roughly two weeks after the census (Fig. 3A), without evidence of depredated or addled eggs that would be indicative of an active nest. This may suggest that the censuses may have included “practice nests” of juveniles or adults, who later sporadically abandoned or reoccupied rock piles. We recommend that researchers surveying newly formed colonies conduct multiple censuses at various times of day, including at the warmest part of the day when penguins may not be sitting as tight to the nest, and/or over multiple days.

Breeding Habitat Preferences

Along the WAP, Gentoo Penguins often breed near glaciers (Herman et al., 2020). Until recently, Biscoe Point (now an island) was joined to Anvers Island by an ice ramp (Antarctic Treaty Consultative Meeting XLIV, 2014), and it has ample rocky habitat (area = 0.48 km²). Point 8 (0.05 km²), Patterdo Island (0.007 km²), and Parmelee Island (0.016 km²) were also relatively recently deglaciated but have more limited space.

First colonizers have the advantage of selecting the most favorable nesting habitat, such as higher elevation regions. Penguins require availability of small nesting stones in quantity. Ridges accumulate less snow and receive greater wind exposure, which enhances snow melt (MacDonald et al., 2010; Marks & Winstral, 2001), providing early access to rocky substrate. Glacial retreat exposes glacial till and morainal deposits, which also provide nesting material (Benn & Evans, 2014). Predation may initially be lower, as other seabirds have yet to establish nest sites (Appendix 1) and nearshore waters may be less frequented by predatory leopard seals *Hydrurga leptonyx*.

The Gentoo breeding colonies in the Joubin Islands are located far from an actively retreating glacier but may provide better access to open water during winter, considering that SIC was higher and more persistent in the 1970s. On Joubin Island 8, penguins occupy nearly all available rocky habitats that are snow-free in the spring, potentially reaching carrying capacity, which perhaps forced breeders to establish a new colony at nearby Joubin 20. Their breeding success in the first year of nesting implies that the colonizing birds were older, experienced breeders, supporting the idea of nesting habitat saturation elsewhere.

At the two largest and longest-established Gentoo Penguin breeding colonies near Palmer Station (Biscoe Point and Joubin 8), Gentoo Penguins first nested within decreasing Adelie Penguin colonies (W. Fraser, personal observation). This afforded them space, nesting stones, and likely some protection from predatory Brown Skuas. This supports the importance of key variables we identified at newer colony sites: less avian predation, available nesting material, and uninhabited, snow-free rocky habitat. It is probable that colonization can happen in multiple ways and depends on environmental conditions. In the 1970s and perhaps to the early 2000s, conditions in the Palmer region were at the limits of this species’ optimal habitat envelope (Cimino et al., 2013), leading to Gentoos selecting nesting habitats where Adelie Penguins were already established. Currently, conditions in the Palmer region are well suited to Gentoo life history, perhaps making most habitats suitable for nesting as long as a few basic environmental conditions are met.

CONCLUSIONS

While mechanisms of range shifts and associated population growth remain uncertain, penguin colonization may happen more quickly than previously thought (Herman et al., 2020). Within three years from glacier recession in 2020 and 4.5 years from initial occupation in 2019, Gentoo Penguins established a new breeding colony at Point 8. It took ~14 years for Gentoos to establish larger colonies and rear chicks at Patterdo and Parmelee Islands, while chicks were reared in the first year of observation at Joubin Island 20. Near Point 8 and Patterdo, other islands host ~1,000 Adelie Penguin breeding pairs (Schofield et al., 2024), suggesting competition for prey resources could occur (Cimino et al., 2016). The influx of ~1,000 Gentoo Penguins substantially increases the number of penguins foraging in the same region. However, the establishment of new and growing Gentoo Penguin colonies suggests that adequate resources are currently available to satisfy both species populations. Continued monitoring, biologging, genetic studies, and banding of juveniles could further inform these changes, and we expect that as researchers keep looking, other unknown Gentoo colony locations will likely be discovered along the WAP.

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AUTHOR CONTRIBUTIONS

MAC: Conceptualization; data curation; formal analysis; funding acquisition; investigation; methodology; project administration;

resources; supervision; visualization; writing—original draft. PK: Data curation; formal analysis; methodology; visualization; writing—review & editing. GL: Data curation; formal analysis; investigation; methodology; supervision; visualization; writing—review & editing. WF: Investigation; funding acquisition; resources; writing—review & editing. DWJ: Funding acquisition; resources; supervision; writing—review & editing. DPF: Data curation; investigation. DR: Data curation; investigation; writing—review & editing. MR: Data curation; investigation; writing—review & editing.

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