PAGOPHILIC RATHER THAN SEA-ICE OBLIGATE: EFFECTS OF SEA ICE AND COLONY SIZE ON ADÉLIE PENGUIN MOLT LOCATION

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ABSTRACT

Strongly pagophilic, the Adélie penguin *Pygoscelis adeliae* has long been designated a sea-ice obligate species, which included the requirement to find pack ice on which to molt. However, observations have accumulated over the years to question this attribute and, therefore, we investigated this aspect of the species' natural history strategy through a synthesis of published, unpublished and historical records obtained Antarctic-wide, and 12 years of time-lapse camera observations at Cape Royds (Ross Island, Antarctica). We describe patterns of molt habitat use at Cape Royds and evaluate whether interannual variation in regional sea-ice conditions (which include at Cape Royds both fast ice and pack ice) during the month immediately preceding the molt season (January) is associated with the number of penguins observed molting at the colony (February). At Cape Royds, automatic camera data, 2008-2024, showed interannual variability in both the timing and numbers of molting penguins. Peak numbers in view of the camera ranged from 75 to 590 individuals (7-30% of the breeding population); timing of the peak ranged from 23 February to 2 March, although date of the last molting penguin was consistent among years (16-17 March). Based on results from a negative binomial generalized linear model, peak on-land molt counts varied negatively with mean January sea ice concentration (SIC) within the colony's foraging area, and with breeding population size (breeding pairs; more breeders, fewer molters). Though a longer time series might supply more definitive indications, there was a ~2.2% decrease in numbers molting per 1% increase in SIC. Supplying context to Cape Royds patterns, review of the literature revealed marked geographic heterogeneity in molt habitat, affected by whether sea ice is present during the molt season (February-March), colony size and access to prey: at some colonies most individuals return to molt on land (including landfast ice) or coastal glaciers, while at others only a fraction do so, and at several large colonies molt appears to occur primarily in distant pack ice. Earlier qualitative interpretations in the literature suggested that greater SIC promotes on-land molting, but at Cape Royds higher January SIC brought fewer molting penguins. Together with the broader circumpolar evidence, these findings suggest that Adélie penguin molt habitat is more context-dependent and variable than implied by a simple obligate sea-ice paradigm. This plasticity, which applies as well to other life history patterns, likely contributes

to the species' ecological success and persistence across annual- to millennial-scale contrasting sea-ice regimes.

1.0 Introduction

> "The evolutionary change of petrel-like avian species into penguins required some amazing physical, physiological and behavioral changes …. Among these …. was the development of special feathers, but then, too, the method by which they are maintained as well as the method of being replaced. Penguins are in trouble unless their feather 'coat' is in perfect working order. Penguins are among the very few avian species that replace their feathers all at one time (except for face feathers among a select few subadults). They have to do this because, needing the magical properties of their special feathers, they can't deal with the ocean with old, worn ones" (excerpt from Ainley and Wilson, 2023: Chapter 2, p. 42).

Penguins, despite being birds, can hold their own in the sea, in many cases surpassing full-time sea creatures in their speed and maneuverability (Ainley and Wilson, 2023: various chapters). One reason for this capability is their feather coat, which by its nature reduces surface tension to greatly reduce drag to near zero, helps to insulate them from the cold sea and aids in their ability to vary their buoyancy. Except for two, the emperor penguin *Aptenodytes forsteri* and Adélie penguin *Pygoscelis adeliae*, all penguin species molt exclusively on land, usually at or close to a breeding colony. The latter generally proves to be the safest, most accessible place to reside for the few weeks necessary to entirely shed and replace their coat. As summarized in Ainley and Wilson, 2023: chapter 2), molt requires 3-4 weeks during which the penguin does not enter the sea. Therefore, post-breeding and before the molt, they forage vigorously to regain body-condition lost during breeding and then to accumulate the fat reserves needed during the molt-fast. This foraging is generally done in the vicinity of where they will eventually molt (see Discussion).

One exception to the penguin generalities regarding molt, the emperor penguin, lacks the agility to access much of the limited exposed land in coastal Antarctica and so, while they can molt in a variety of habitats, they mostly are confined to access sea ice of low enough freeboard that they can manage the necessary leap, for both breeding and to molt (e.g., Kooyman et al., 2000; B. Weinecke, pers. comm.). Generally, that is sea ice that formed earlier in the same year, i.e. annual sea ice, with the ice forming as a continual sheet close to the continent and then breaking into ice floes owing to waves as the wind blows it northward. Ice that is in protected areas remains locked in place as landfast ice (fast ice), where it thickens.

The other, partial exception, is the Adélie penguin, another strongly pagophilic species but whose life history strategy is plastic enough, and the species is agile enough, that it can molt either on land, landfast ice (fast ice), low freeboard coastal glaciers, or compacted floes of pack ice (both annual and multiyear), as long as that ice is substantial enough that it will not dissolve or break-up during the required molt period, which typically lasts 15-25 days (Cendron,1953; Gain, 1914; Penney, 1967; Takahashi et al., 2018; Schmidt et al., 2023; Zajková et al., 2025). The ice also needs to be old enough (usually multi-year) that it has high pressure ridges to provide wind protection as well as snow drifts that provide fresh water (D. Ainley, W. Fraser, pers. obs., based on multiple cruises within pack-ice covered ocean; also Cline et al., 1969). Recently, researchers have begun to question whether the lessening sea ice extent (generally annual ice) in the Southern Ocean, which has been observed since about 2016 (Parkinson, 2019; Diamond et al., 2024; Maksym and Stammerjohn, 2025), might negatively affect Adélie penguins, in the context of whether the availability of sea ice on which to molt could be problematic (Schmidt et al., 2023; Zaldua et al., 2024). This questioning has as its basis the long-held paradigm that the Adélie penguin is an ‘ice obligate’ species (more below).

In decades past, based on what can be inferred from the minimal research effort that historically had been expended on this species, it was thought that, in accord with its supposed sea ice dependency, post-breeding Adélie penguins seek sea ice, especially pack ice, for a platform on which to molt (e.g., Sladen, 1958; Ainley et al., 1983; Ainley, 2002). After all,

Antarctica for most of the last ~200 years of human contact and exploration has been very difficult for researchers to access, especially outside of the mid-summer season. Observations of penguins for the longest time were few, especially after the penguin breeding season ended. However, with the proliferation of research stations following the International Polar Year in 1957-58, and negotiation of the Antarctic Treaty in 1959, research on Adélie penguins proliferated --- like these penguins, humans are attracted to coastal, ice-free land, a limited commodity, on which to build permanent bases. A close association thus was initiated. Hundreds of studies of Antarctic penguins, especially involving Adélies, have since accumulated (e.g., Ainley, 2002; Ropert-Coudert et al., 2019). Other than proximity to research facilities, the intensive study effort is also a function of this species very large population (3.8 million pairs at ~250 colonies which, including non-breeders, amounts to ~10 million individuals; Lynch and LaRue, 2014).

This impressive research effort has revealed the Adélie penguins' 'love-hate' relationship with sea ice, and that the type of ice matters: open water vs pack ice vs fast ice. On the basis of at-sea surveys, the Adélie penguin was found to be a member of a species group that is strongly, and almost strictly, associated with pack ice or sea-ice-influenced ocean, i.e. an extremely pagophilic community (Ribic and Ainley, 1989). A 'natural experiment' in the Scotia-Weddell Confluence confirmed the latter correlative observations --- repeatedly over several weeks whenever the wind shifted from a direction expanding the pack ice field north 50-100 km to a direction causing the pack ice field to contract south, within that dynamic stretch of ocean, the sea ice species group, moving with the pack ice, replaced the open water species group (including the congeneric chinstrap penguin, *P. antarctica*). In the common stretch of water, both species groups foraged on the same prey (Ainley et al., 1993). This indicates that the physical nature of the habitat, specifically the presence of sea ice, is the primary driver of species community membership.

The opposite of this pagophilic connection are species' ranges that does not include waters/regions where sea ice is absent, at least at the large scale (map in Ainley and Wilson,

2023). At the local scale, since Adélie penguins would rather swim than walk, sea ice too concentrated, especially fast ice (100% cover), leads to dramatically reduced breeding numbers and even emigration (Jenouvrier et al., 2005; Massom et al., 2006, Dugger et al., 2014). On the other hand, the species depends on the presence of open water adjacent to colonies, i.e. polynyas, for colonies to exist (Santora et al., 2022). Trends in the seasonal growth and timing of polynya openings in the pack ice affect whether colonies grow or retract in size (Emmerson and Southwell, 2022; Ainley et al., 2024).

Lagging behind the impressive effort to quantify Adélie penguin breeding biology, however, has been attention to the several months of non-breeding in the species' annual cycle, spent in the pack ice. Recently, with miniaturization of data loggers, investigations have broadened to look at post-breeding/wintering aspects (e.g., Ballard et al., 2010a; Jongsomjit et al., 2024; Zaldúa et al., 2024; Zajková et al., 2025). Since the species' wintering habitat is at sea in the pack ice, what is required is better understanding of what factors affect the species during its non-breeding season.

In order to contribute toward understanding the Adélie penguin connection to sea ice, in particular pack ice, we reviewed the available literature pertaining to the penguins' post-breeding activities, particularly molt. Equally important, we made inquiries to colleagues currently or recently conducting penguin research asking whether they had unpublished information to share. Finally, we present results from an automatic camera positioned full time during 13 years at Cape Royds, Ross Island, Antarctica (Fig. 1). That is where the first observations of this species and its natural history were made (J. Murray *in* Shackleton, 1909), including the first locality where the process of molt was described (Taylor, 1962).

In this paper we address the following three objectives. First, we reviewed the literature, as well as communicating with colleagues, seeking evidence of Adélie penguins molting at colony locations or other areas on land/glacier locations vs on pack ice (land' includes landfast ice; Table 1). Second, we used the camera data to assess the variability of the first and last dates of

molting, and the date of peak number of molting penguins at Cape Royds over the 13-yr observation period. Third, we explored the relationship between the mean daily sea ice concentration (SIC) during January in the foraging area at Cape Royds (Fig. 1) and the peak number of birds eventually (a month later) molting, testing an assumption made by others, that more sea ice at the end of the breeding season brings more molters to a location (Sladen, 1958; Parmelee, 1992; see below). January is when penguins would be assessing their post-breeding strategy, i.e. non- and failed-breeders departing and returning, and then breeders finishing their task, and returning. We hypothesised that SIC during that time would be assessed by the penguins, deciding whether it should be negotiated for a return visit to the colony in order to molt.

2.0 Methods

2.1 Study Site

Cape Royds (77°33'S, 166°10'E) is on the southwest coast of Ross Island, on the shore of McMurdo Sound (Fig. 1). It is the southernmost Adélie penguin colony (Lynch and LaRue, 2014), and the site where Ernest Shackleton's *Nimrod* Expedition built a hut and occupied it 1907-1909 (Fig. 2). More recently, research has been conducted there periodically, beginning in 1955 and continuously since 1995 (Ainley et al., 2024). Note that, in the following text, each austral summer breeding season (including molt period) is identified by the initial year, e.g. November 2008 (egg laying/incubation) through January (chick provisioning/fledging) to February/March 2009 (molting) is identified as the 2008 breeding season.

Since 1955, the size of the Royds colony has been assessed annually in the first week of December, via direct count of occupied nests, aerial photography (Antarctica New Zealand) and, beginning in 2018, also by drone photography (Lyver et al., 2014; Ainley et al., 2024; Shah et al. 2020). During most years, hurricane-force winds blow periodically from the south, especially prior to and in the early breeding season, thus generating the McMurdo Sound Polynya (Arrigo et al., 2015), the factor behind existence of the colony (Stonehouse, 1970). However, the terrain

at Cape Royds has substantial ridges that provide a lee for both penguins and the hut (Fig. 2), though the penguins choose the wind-swept portions for breeding. Subcolonies were counted on about 1 December each season directly, to ground-truth the aerial counts. The number of chicks that survive to creche age, as counted 12-15 January and the ground-truthing counts, provided an estimate of chicks/pair at about that age when chicks become large enough to move away from nests (creche stage). The chicks/breeding pair ratio provides an indirect index of the prevalence of failed breeders (lower value of chicks/pair indicates more failed breeders). The failed breeders leave the colony a few weeks before breeders (Ainley, 2002).

In 2008 (until 2010), a 'Penguin Cam' (PCam) was set up on an anchored instrument tower, along with an electronic weather station (Figs. 2, 3). During these three seasons, the camera's viewscape was of Shackleton's hut and the physiographic 'bowl' in which it was built. The camera was located on a slope above the hut, looking down ~15 m away, and so its field-of-view included just the hut and the lee of the ridge immediately to its south where some birds also molted (Fig. 2). The former horse-pen, built on the lee side of the building, over the years filled with feathers. Indeed, it was in part the accumulation of feathers, perhaps a meter deep against the north-facing wall of the hut, that in part led to the 'infection' by mold of the hut's Scotch pine wood. That in turn led to the Antarctic Heritage Trust rebuilding the hut and conserving its artifacts during 2004-2010. The Trust's activities generally ended before the molt season.

In a few successive years, construction continued into February, discouraging penguins from molting in the hut's lee at least during the early molt season. After a year of no PCam, in 2012 (until 2024) the camera system was moved to a position southwest of the hut. The viewscape, from about 100 to 130 m away, then included two-thirds of the colony area, at the base of a ridge that offered protection; just below the ridge crest is where the penguins chose to molt (Fig. 2). The new camera view was looking across several subcolonies and up at the sheltering ridge and, thus, field-of-view was much greater than at the initial deployment location. Every day at 15:00 local time (same as NZ time) the PCam took a series of overlapping images (5 frames) across sequential portions of the viewscape. Each frame covered ~50 m wide partially,

overlapping segments of the ridge. The solar-powered camera was activated just prior to expected arrivals in late October and deactivated after the last molting penguin departed in the following March.

Molting penguins were counted in the images (by DGA; Supplementary Material Tables A1, A2). Gaps in counts occurred periodically owing to bad weather ('white outs'), fogging of the camera dome (if weather became warm, humid), dirt/snow accumulation on the protective dome (leading to camera focusing on the dirt), malfunctioning of the system (all photo frames sometimes not available), or counter pre-occupation with other activities (see Limitations of the Study). The system was completely inoperative in 2015 and was minimal from 2020 to 2023 as a consequence of COVID limitations on research in the USA Antarctic program. Hence, during those years, there was little attention given to up-keep. It ceased operation part way through the 2024 molt season.

2.2 Literature Search

The authors, with their respective decades of research in penguins, had an appreciable library of relevant papers. However, to try not to leave any important studies out, literature relevant to Adélie penguin molt was retrieved programmatically in R from three bibliographic databases: Scopus, Semantic Scholar, and Google Scholar. Search queries combined species terms with molt-related terms across eleven languages (English, French, German, Spanish, Italian, Polish, Norwegian, Japanese, Korean, Chinese, and Russian) to maximize international coverage (translation services provided by Google Gemini). Each database was queried through its respective application programming interface, with pagination used to retrieve all available results. Retrieved records were filtered to retain only those in which both a species term and a molt term appeared in the title, abstract, or keywords. Records were then assigned a relevance tier based on where the terms co-occurred: tier 1 (both terms in the title), tier 2 (terms split across title or keywords and abstract), and tier 3 (both terms in the abstract only). Duplicate records appearing across databases were removed, retaining the version with the highest-quality metadata, prioritizing Scopus, then Semantic Scholar, then Google Scholar (due to

relative quality of data with regards to formatting). The final deduplicated record set was exported for manual review, sorted by relevance tier.

A total of 189 entries were identified. These were winnowed, deleting citations that proved to not contain relevant information; ultimately 8, from the literature search, provided citations we would not have otherwise included.

2.3 Penguin Cam Particulars

The PCam system was developed as a remote monitoring solution aimed at observing penguin activity at the Cape Royds colony during summer, including after researchers departed (Fig. 2). Visitors to the penguinscience.com website could have daily views of much of the colony. The creation of such technology, including systems deployed by others elsewhere, marked a significant advancement in automated wildlife observation in the challenging environmental conditions of Antarctica.

The first version of our system was deployed in 2008 at a location ~15 m north of Shackleton's Hut (Fig. 2). Field of view was mostly just of the hut, as the camera was only ~25 m from it. The system was designed to operate in all weather conditions and included several specialized components, including an all-weather sensor (Vaisala), a GPS receiver for timestamping data, a Sony PTZ camera, and a small Linux computer to manage operations. Power was provided by two solar panels that charged three batteries, ensuring the system's autonomy. To facilitate the uploading of data and photographs, an Iridium modem was integrated into the system. The main goal of the initial PCam deployment, other than website viewers seeing some penguin activity, was to capture photographs of penguins during their end-of-season gathering, which takes place in the lee of Shackleton's Hut. This objective was successfully achieved in the first season, demonstrating system effectiveness. The PCam was programmed to automatically take photographs once per day and upload these images to a dedicated website (penguinscience.com).

In 2012, with permission from the US and NZ Antarctic programs (see Acknowledgements), the PCam system was moved to a location just inside the boundary of the protected colony zone (Fig. 2). The camera was now 100-130 m away from the penguins, providing a much wider overall viewscape than in its previous location. The aim was to enhance monitoring of a large portion of the colony and to better support research and education objectives (visitors to the penguinscience.com website could see daily images of the colony). Combined with the resolution of the Sony camera, the distance between it and the colony, allowed researchers to count individual penguins.

The upgraded system included the addition of a Nikon DSLR D90 camera mounted on a pan and tilt stage, as well as a second Linux computer to control and manage the photographs taken by it. During the period from about 20 October to mid-March, a series of photographs spanning from left to right (5 frames) were captured once daily and uploaded to the website (penguinscience.com). Each photo captured about a 50-m expanse of the ridge where the penguins molted; most of the molters were in the first three, southeast-most views; Fig. 4 shows the fourth, to the northeast; with the fifth usually having just a dozen molters). On clear days, with sunlight behind the PCam, the system was able to capture exceptional photographs of the colony. From 2012 onward, the system remained largely unchanged, aside from necessary maintenance carried out over the following years. As noted above, the system was inoperative in the 2015-16 austral summer and became so part way through the 2024 molt season (Supplementary Material Tables A1, A2). Therefore, while the camera was present during 13 seasons, we did not use the partial season of 2024 in our analysis.

2.4 Measuring Sea Ice Concentration in McMurdo Sound

The northern, seaward edge of the extensive fast ice that covers the southern portion of McMurdo Sound, at least through the penguin breeding season each year (Kim et al., 2018), is at Cape Royds (Fig. 1). North of that edge is the McMurdo Sound Polynya, which is completely open water or has loose pack ice (Arrigo et al., 2015; Ainley et al., 2024). If southerly winds are persistent, which is the norm, the portion of the Sound north of the fast ice is blown free of

pack ice or, in some years, even of landfast ice (in years when more extensive than usual). If winds are from the north, then ice in the area is pushed south packing floes together against the fast ice edge, with the then consolidated pack sometimes extending several kilometers north. We assessed sea ice cover (SIC), i.e. prevalence of the pack ice in the middle portion of the Sound (the seascape in view from our Royds camp on a hill above the colony). This was done for each day during January using satellite imagery. Our purpose was to determine whether SIC affected the number of birds molting at Royds, as has been proposed for other locations (Sladen, 1958; Parmelee, 1992).

Using daily values, we generated a time series of mean January SIC (percent concentration) within the primary foraging area of the Cape Royds Adelie penguin colony, as determined during the chick-feeding seasons between 2002 and 2014 (see next section). This dataset included 4341 locations from 67 breeding individuals tracked using Wildlife Computers SPLASH tags, with positions provided by the Argos system (positional error estimates range from 100 to >1000 m). Foraging areas extended along the fast ice edge and north for several kilometers (Ford et al., 2015; Saenz et al., 2020). Results were consistent with previous evidence obtained using radio telemetry (Ainley et al., 2004).

2.4.1 Sea Ice Concentration Analysis

We obtained daily SIC data from the University of Bremen (seaice.uni-bremen.de), specifically the AMSR-E and AMSR2 ASI product (version 5.4), which uses the ARTIST Sea Ice (ASI) algorithm (Spreen et al., 2008). This algorithm relies on the difference between the 89 GHz vertically and horizontally polarized brightness temperatures, providing a 3.125 km spatial resolution (grid cells of 3.125 X 3.125 km). The algorithm incorporates weather filters and comparisons with the Bootstrap algorithm (which uses lower frequencies) to reduce spurious ice detection due to atmospheric effects. The resulting daily data are provided in a standard NSIDC polar stereographic projection (EPSG:3412 for the Antarctic grid). The reported accuracy of the ASI algorithm varies with SIC; the absolute error is estimated to be approximately 25% at 0% ice concentration, decreasing to less than 10% for IC values above 65%.

For each year in our study, all daily sea ice rasters for 1-31 January were processed. Each raster was processed to set invalid data (e.g., land, pole hole, missing data, values 100%) to Not Available. Data were not available for 2011 due to a gap in satellite coverage.

We calculated a single mean SIC value for each January of each year by averaging all valid pixels within the polygon (terra:extract(..., fun = 'mean')), from which SIC values were generated for each year: the overall mean, standard deviation, and standard error. The count of valid rasters (days) used for this calculation was recorded as 31 for all years. We also determined a value for 15 January, which was typically the last day we were present at the colony each season.

2.5 Overall Data Analysis

Gaps in the PCam coverage were frequent enough that it was possible only to reveal the general pattern of penguin molting, e.g. insight into first and last presence, peak presence etc. Interannual variation in those observations was apparent, though the factors behind the variation were challenging to elucidate. Daily, we recorded the weather, both directly from a hut-based meteorological system as well as from instruments on the PCam tower.

We assembled a season-level dataset in R (R Core Team, 4.5.1.), from the camera counts (molt dates and the peak count per season) and merged these with Table 2 covariates (sea-ice, colony size, chicks/pair). The response variable for the focal analysis was ‘peak_molt,’ defined as the maximum number of Adélie penguins observed simultaneously molting on land during that season. Predictor variables included (1) mean January SIC (sic_all; %), derived from satellite imagery as described above; and (2) colony size, expressed as the number of breeding pairs and log-transformed to linearize scaling effects.

We included mean January SIC as a predictor because, as we hypothesized, the presence of sea ice during the late breeding period, beginning with the departure of non-breeders, may influence whether individuals return to molt in the vicinity of Royds. Colony size (number of

breeding pairs) was included, given that reproductive status constrains molt timing and may affect the likelihood of returning to the colony to molt.

To assess whether relocation of the camera system influenced statistical inference, we conducted a sensitivity analysis using the same 12-season dataset included in the final model. We compared the pre-specified negative binomial model of peak on-land molt counts as a function of mean January SIC and log-transformed colony size with an alternative model that additionally included camera position (Hut vs. Colony) as a fixed effect. Models were compared using a nested likelihood ratio test, and we assessed whether inclusion of camera position materially altered the estimated coefficients for sea ice concentration and colony size. Descriptive summaries of peak molt counts, SIC, and colony size were also calculated separately for hut- and colony-view seasons.

The sensitivity analysis showed that adding camera position did not improve model fit (LRT = 0.95, $p = 0.330$), the camera term itself was not supported ($\beta = 0.31 \pm 0.30$ SE, $p = 0.303$), and inclusion of camera position did not materially alter the estimated effects of SIC or colony size. For this reason camera position was not included in the final inferential model.

Following the inference-focused framework of Tredennick et al. (2021), we treated model selection as a hypothesis-driven inference problem rather than an exploratory variable selection exercise. We therefore specified a small, mechanistically motivated candidate model *a priori*, including sea ice and colony size.

We fitted a negative binomial generalized linear model with a log link using the function glm.nb() in the MASS package:

peak_molt~sic_all+log_colony (log_colony is the natural log of breeding pairs)

Model diagnostics were conducted using the performance package. Overdispersion was evaluated with *check_overdispersion(),* and multicollinearity was assessed using *check_collinearity()* (variance inflation factors). The contribution of each predictor was

evaluated using likelihood ratio tests via drop1(..., test = "Chisq"), comparing nested models (aligned with inference-first testing recommended for small candidate sets; Tredennick et al., 2021).

We report effect sizes on the natural scale as percent change per unit increase in the predictor: $\%\Delta=(e^{\beta}-1)\times100$. For log_colony, we interpret effects for a doubling of colony size (breeding pairs) by scaling β by log (2).

3.0 Results

3.1 Insights from the Penguin Cam

During the first few days of the molt season, it was difficult to distinguish molting adults from the few-remaining large, yet-to-fledge chicks. The latter, however, moved around day-to-day, unlike molting adults, and soon departed. In addition, these chicks remained in the vicinity of their nests, populating the lower, wind-swept portion of the PCam view. Molters concentrated along the ridge, sheltered from the wind, above the breeding subcolonies, and were separated from most of the large chicks that were present. The earliest molting adults were detected on 2 February at the Hut and 1 February in the colony (Supplementary Material Tables A1, A2). It was relatively straightforward to count molting adults when vision was unrestricted, as molting Adélie penguins did not clump (Fig. 4). Molters concentrated in several extremely protected locations, the same ones every year, though not all of them in the PCam viewscape. Peak numbers of molting birds that could be photographed varied in timing from 23 February to 2 March at Shackleton's Hut, 2008-2010, and 20 February to 2 March in the colony, 2012-2024 (Figs. 5; Supplementary Material Tables A1, A2). The last molting birds at each were detected on 14 to 17 March, in both areas, depending on year. Thus, the end of molt was slightly more constant than timing of the peak (which varied over two weeks).

Within the camera view, the peak number of penguins varied, with values at the Hut vs colony view being, 251-415 and 126-590, respectively (Table 2, Fig. 5). We assume that penguins

molting at the hut were separate from those along the colony ridge, although at times during the second deployment, when there were distinct jumps in numbers, a group of molters had arrived from beyond the camera's view. Since we only had one camera setup we could not assess whether penguins molting at hut had moved. As noted in Table 1, there were other locations on the Royds Peninsula and the nearby vicinity where molting also occurred, e.g. Black Sand Beach, and there were at least two sheltered molt locations within the colony that could not be seen by the PCam. When we arrived each spring we found guano deposits and piles of feathers in those locations, showing that an unknown number of penguins had molted there. Considering the maximum counts at both locations (max 415, 590; mean 334 and 300; Supplementary Material) and knowing that others were molting in the vicinity that were outside PCam view, we surmised that respective camera views included ~50% of the total molters on the Cape Royds peninsula. Doubling that count is consistent with the estimate of ~800 made by Austin (1957; see also Yeates, 1968) for the entire peninsula, the size of the colony population being slightly smaller than it was during our study; Taylor (1962) reported 540, but at a timing a couple weeks short of when the maximum would have occurred during his year of study. We used our 50% estimate to assess variation in the approximate ratio of the numbers molting birds relative to breeding population size (Table 2).

Using this approach, the ratio of molting numbers to breeding numbers varied from 6% to 30% (Table 2). Of course, the estimate of occupied nests on about 1 December each year does not include non-breeders (that generally leave for a while prior to then; Ainley, 2002). Thus, those percentages possibly should be reduced to include a larger total colony size, ~5-20%.

The inferential model was fitted to all seasons with complete data on peak on-land molt counts, mean January SIC, and colony size (n = 12 seasons). These included both hut-view (2008–2010) and colony-view (2012–2023) camera periods. Peak on-land molt counts varied markedly across seasons (range: 75–590 individuals), indicating substantial interannual variability in the maximum number of Adélie penguins molting simultaneously on land at Cape Royds.

Model diagnostics indicated no evidence of overdispersion (dispersion ratio = 0.81, p = 0.90) and low multicollinearity between predictors (variance inflation factor, VIF = 2.25 for both terms).

In the pre-specified negative binomial model, mean January SIC was negatively associated with peak molt counts (β = –0.022 ± 0.011 standard error, SE, z = –2.06, p = 0.039; Table 3), which corresponds to an approximate 2.2% decrease in peak on-land molt counts for each 1% increase in SIC (Fig. 6).

Likelihood ratio tests (LRT) confirmed that the removal of SIC significantly reduced model fit (LRT = 4.53, p = 0.033). Colony size was also negatively associated with peak on-land molt counts (β = –1.94 ± 0.99 SE, z = –1.96, p = 0.050). On the original scale, this indicates that years with higher numbers of breeding pairs exhibited lower maximum numbers of individuals molting simultaneously on land. Likelihood ratio tests supported the inclusion of colony size in the model (LRT = 4.70, p = 0.030).

3.2 Insights from Literature and Unpublished Information Review

Biologists have stayed long enough at only a few of the ~250 known Adélie penguin colonies to determine how many penguins subsequently returned to molt at the colony or in its vicinity. Therefore, there are relatively few observations to deduce the degree to which this species molts on land (at colony or nearby) --- the information that exists indicates a range from all to none, as well as molting on land or a low freeboard glacier elsewhere (Table 1). Indicating that molting at the colony in some cases does occur is provided, indirectly, by the summary of dates when penguins finally departed the colony done by Marchant and Higgins (1990; see references therein): Cape Adare, 14 March; Paulet Island, a few days after 15 March; Davis, 10-31 March; Haswell Island, late March. For Cape Hallett, Reid (1964: p 14) reported that on 7 March 1961, “only a few hundred moulting adults remained.” The end dates for these various locations are

485 more than a month after the breeding season is finished. Below, we are more specific in our
486 findings from the literature search.
487
488 At Arthur Harbor, site of Palmer Station on the central west coast of the Antarctic Peninsula,
489 biologists over-wintered for about 10 years during the 1960-70s. Judging from various data
490 sources, including censuses and banded bird sightings, it appears that most birds molt at
491 the colony (~20,000 pair) or vicinity (36,000 for Palmer Archipelago (Poncet and Poncet 1987)
492 as suggested by Parmelee (1992); W. Fraser, pers. obs). However. a significant number also
493 molt elsewhere at other colonies (see below; Table 1). Using another data source, namely
494 the recovery of molted presence/absence transmitters used in foraging studies (Fraser and
495 Hofmann, 2003), W. Fraser (pers. obs.) notes that, of 163 recovered tags spanning the years
496 1990-2019, 110 (67%) were recovered where they were deployed and 53 (33%) were
497 recovered at locations further south than the Palmer area. This is in accord with numbers
498 of molting birds seen at the more southern colonies, i.e. more molting penguins than
499 respective colony populations (W. Fraser, pers. obs.; P. Convey, pers. obs.; Table 1). In contrast,
500 on Signy Island, at an even lower latitude (60°S, north of the Antarctic Circle), according to
501 Clarke (1906) and Sladen (1958), all Adélie penguins apparently departed, followed by molt
502 presumably in the pack ice, which at that time of year still exists to the south some ~300 km
503 away. However, at least in recent years as the number of penguins on the island has decreased,
504 this pattern is no longer the case (Table 1; P. Convey, pers. obs.). This change is discussed in
505 more detail below.
506
507 In East Antarctica, at Murray/Scullin Monoliths in 1931, at least half of the 300,000 adults
508 present were molting, while the other half were still feeding near-to-fledged chicks (Falla, 1937).
509 Since that range of timing has not been reported elsewhere (molting overlapping breeding), it
510 would seem possible that those molters were non-breeders (which molt first) that had arrived
511 from other colonies. Also in East Antarctica, in one year of study (1991-92) at the small colony at
512 Béchervaise Island, within a complex of colonies off the Mawson Coast, numbers of molting
513 birds reached 25% of colony maximum, although observations ceased while numbers of molters

were still increasing (Kerry et al., 1993). Further east, at the Windmill Islands, Penney (1967), who also had banded birds with which to work, estimated that 20% of the colony returned to molt. That proportion appears to have been true also in vicinity of Pt Geologie, farther east. Still farther east, along the Victoria Land coast and islands in the Ross Sea, Taylor (1962), who stayed at Cape Royds until 14 February (at least a week short of when the molting peak should occur (our study)), estimated several hundred molting birds, as have others. He further reported that members of four pairs at 15 closely-followed nests had returned by that date to molt, after their two-week absence to regain condition. Taylor's observations were consistent with those of earlier researchers (Yeates, 1968; Spellerberg, 1971; Table 1). Descriptions of molting populations at other sites are qualitative, e.g. "thousands" molting at breeding colonies such as Cape Adare and Cape Hallett in northern Victoria Land (Levick, 1914; Nevins, 2001; Table 1). A portion of the molters at Hallett were on the fast ice adjacent to the beach. More than 200,000 pairs nest in three colonies between those two locations, but those colonies are rarely visited, if at all, during molt season.

4.0 Discussion

The initial view of Adelie penguins' obligatory need for pack ice on which to molt was formulated by Sladen (1958), who worked at the South Orkney Islands, with the idea adopted by close colleagues. Sladen's view was supported by observations of the penguins at Cape Crozier, Ross Island, where his group subsequently worked during the 1960s to early 1970s, e.g. Ainley, LeResche and Sladen (1983). Here, as at the South Orkneys, the pack ice disappears long before the molt season starts. Moreover, colonies as large as the Cape Crozier colony face significantly depleted prey in their colony foraging area (Ainley et al., 2015). Indeed, breeders feeding their growing chicks must forage increasingly farther from the colony, out to ~180 km (Ballance et al., 2009; Ford et al., 2015; Ballard et al., 2019). Thus, any foraging to recover condition lost during breeding has to take place 300-400 km away from Cape Crozier in shelf break waters off Marie Byrd Land. That area, with persistent, multi-year pack ice, had long been known to support large numbers of molting Adélie (and emperor) penguins (as well as other

543 birds), despite just a few small colonies in the vicinity (Ainley et al., 1984, 1998; see also Ballard
544 et al., 2010a; Schmidt et al., 2023). The Shelf Break Front, present in that location, is extremely
545 productive (Ainley and Jacobs, 1981).
546
547 The same pattern likely applies at Signy Island (South Orkney Islands, where Sladen initially
548 worked), and where not just Adélies breed but also even larger numbers of potentially
549 competing chinstraps, as well as less abundant gentoo penguins, *P. papua* (Woehler 1993); the
550 latter species molt at their colonies on Signy (Warwick-Evans et al., 2019; this is the same
551 pattern among Pygoscelid penguins in South Shetlands: Hinke et al. (2015); Sierakowski et al.,
552 2017). The gentoo and chinstrap penguins are still feeding chicks, i.e. depleting the near-colony
553 prey field, when the earlier-breeding Adélies need to fatten to recover condition. Supporting
554 Sladen, Warwick-Evans et al. (2015) tracked 4-12 Adélie penguins over a span of five years, and
555 all molted south of the South Orkneys in the compacted, multiyear pack ice that typically occurs
556 in the northwestern Weddell Sea (Zwally et al., 1983; Gloersen et al., 1992; Maksym and
557 Stammerjohn, 2025). Similarly, Adélie penguins tracked from the South Shetlands (tip of
558 Antarctic Peninsula) also headed to the northwestern Weddell Sea to molt (Hinke et al., 2015;
559 Zaldúa et al., 2024). Therefore, Cape Crozier, Signy Island and the South Shetlands appear to be
560 similar with respect to molting --- in the consolidated pack ice, a long distance away, owing to
561 insufficient prey near to the colony due to intense intra- and interspecific trophic competition.
562 No more than a few hundred Adélies have been documented to molt at Cape Crozier, one of the
563 largest Adélie colonies (~250,000 pairs); observations there have extended into late-February
564 (Ainley et al., 1978). Where other populations molt is reviewed below.
565
566 Our recent camera observations at Cape Royds closely support those of Taylor (1962) and Yeates
567 (1968, and even Murray (1909). As noted in Table 1, Adélie penguins also molt at other
568 locations in the vicinity. In addition, some breeders molt away from Royds vicinity, e.g. at
569 coastal, probably colony sites in northern Victoria Land; GLS tracking indicated that 29% of Cape
570 Royds tagged breeders (n = 49 tagged) molted along that northern coast in 2017-19 (Schmidt et
571 al., 2023). In those locations, e.g. Capes Hallett and Adare, “thousands” of molting Adélie

penguins have been recorded (Table 1). How that compares to their respective colony populations is unknown, given that these are inevitably qualitative assessments.

Given the 50-day period during which molting Adélie penguins are present at Cape Royds, and the 15–25 days needed for an individual to complete its molt, birds of different breeding status molt here progressively. The first molting penguins would likely be dominated by failed breeders and/or non-breeders, followed by breeders (Sladen, 1958; Penney, 1967). Based on biologging data, Schmidt et al. (2026) reported that average start date of molt for Cape Royds breeders was ~21 Feb during 2017-19, lasting for ~19 days. That is consistent with the observations of Taylor (1962), who was present only until 14 February, before numbers of molting birds likely peaked (thus, others likely returned subsequently). As long as McMurdo Sound remains ice free, regardless of when penguins finish molting, there should be plenty of food available for recovery of condition (see below), given the relatively low number of birds. On the other hand, the penguins would need to vacate the area before full night falls (first sunset 20 February); Adélies prefer daylight for foraging (Ainley and Ballard 2012).

When molting in the pack ice, Adélie penguins frequent areas of compacted, multi-year ice (Cline et al., 1969; Ainley et al., 1998; Takahashi et al., 2018; Zajková et al., 2025; W. Fraser, pers. obs.), which occurs in only a few sections of the Antarctic coast in February. Depending on the year, only a third to a half of the continent's circumference has persistent sea ice, principally in the northeastern Ross Sea/Amundsen Sea, ocean off Terre Adélie, and western Weddell Sea (Zwally et al., 1983; Gloersen et al., 1992; Maksym and Stammerjohn, 2025). Yet the ~250 Adélie penguin colonies encircle the continent (few colonies along ice-bound coasts; Woehler 1993; Lynch and LaRue, 2014; Santora et al., 2020). Breeding Adélie penguins from Cape Crozier mostly molt in the persistent pack ice of northeastern Ross/Amundsen Sea (as noted); penguins from Île des Pétrels, Pointe Géologie, molt in the pack ice that remains to the west off Terre Adélie/Wilkes Land (Zajková et al., 2025); and those from northern tip of Antarctic Peninsula (and South Orkneys) molt in the persistent pack ice in the northwestern Weddell Sea (Zaldúa et al., 2024; noted above). Clearly, if molting on sea ice was obligatory,

601 Adélies at many colonies, the extreme being the colonies on the remote South Sandwich Islands
602 (north edge of Adélie penguin range), would have to travel 1000s of km to find suitable pack
603 ice, far longer than even the penguins from Signy Island or Cape Crozier undertake (~400 km).
604 Along the few hundred kilometer stretch of coast bordering the Barrier Bay Polynya, east of
605 Prydz Bay, Adélie penguins were found molting along the edge of the long-grounded D-15
606 iceberg, which slopes gradually into the sea (Table 1; B. Wienecke, pers. comm.).
607
608 **4.1 Factors Affecting Where Adélie Penguins Molt**
609 The sampling of colonies contained in Table 1 indicates a higher likelihood of penguins molting
610 on land/glaciers along those stretches of coast having little or no pack ice during molt season,
611 including much of western Antarctic Peninsula, East Antarctica and western Ross Sea. At a
612 smaller spatial scale, the factors that affect the number of penguins molting at a land (or glacier)
613 site can, however, only be surmised. Based mostly on a review of the literature, Sladen (1958)
614 noted that in localities other than the South Orkney Islands the degree to which the respective
615 Adélie penguin populations molted on land was greatly affected by the presence, or lack
616 thereof, of pack ice in the vicinity --- more ice, more penguins molting. This pattern was also
617 reported by Parmelee (1992) for Arthur Harbor. Contrary to the pattern proposed by Sladen
618 (1958), our quantitative analysis at Cape Royds indicates that higher January SIC leads to lower
619 peak numbers of molting Adélie penguins. Specifically, we estimated an approximately 2.2%
620 decrease in peak on-land molt counts for each 1% increase in mean January SIC. Within the
621 limits of this 12-season time series, this pattern suggests a negative association between
622 regional sea-ice presence and on-land molting at least for Cape Royds. It is perhaps pertinent
623 that both Sladen (1958) and Parmelee (1992) worked at locations where sea ice seasons were
624 short, so little if any pack ice was present before or during molt season. At Cape Royds,
625 however, extensive sea ice usually remains well into molt season.
626
627 One potential explanation for the pattern at Cape Royds is behavioral and energetic rather than
628 strictly based on habitat-limitation. After breeding, individuals must replenish substantial body
629 reserves lost when breeding and prior to initiating molt (discussed further in next section).

When extensive sea ice is present during this recovery period, penguins departing from the colony may remain on pack ice to undergo their molt rather than return to land --- a matter of convenience? In this scenario, sea ice does not facilitate on-land molting. Instead, it provides an alternative molting platform, thereby reducing the number of individuals returning to the colony to molt. However, a far more likely explanation is that the rough, treacherous nature of compacted pack ice, i.e. many tilted ice floes require each to be climbed, would discourage penguins from trekking back to the colony. The rough ice surface does not allow the penguins to toboggan. Also, there are at least some leads in which predatory leopard seals *Hydrurga leptonyx* lurk, providing further disincentive for the penguins to return to the colony. When approaching a lead, penguins tend to wait many hours until they deem it safe to dive into the water; thus, progress is slow. Faced with such pack ice conditions, on their departure from Cape Royds, they could have chosen to molt farther north.

The size of the Cape Royds colony, i.e. number of breeders, was also negatively associated with peak on-land molt counts. In years of greater colony size, a lower number of individuals molted at Cape Royds. This pattern may reflect the constraints imposed by reproductive status: breeders typically initiate molt later than non-breeders and may be under pressure to make their way north from this southernmost breeding colony to avoid being caught in the dark (Ainley and Ballard, 2012). It is also possible that in years of higher breeding numbers there is less food available near the colony, although we have not observed evidence of prey-depletion at this relatively small colony (Saenz et al., 2020).

Together, these findings refine earlier qualitative interpretations and suggest that environmental context shapes the expression of molt for a given colony of Adélie penguins. Other ecological factors likely modulate this spatial expression.

4.2 Characteristics of Adélie Penguin Molting Habitat

4.2.1. Sheltering. Shelter from wind is important for molting birds on land (or on sea ice), indicated by molting individuals consistently aggregating in protected areas at Cape Royds and

other sites. Likewise, food and drinking water availability during the post-breeding recovery period may influence where birds ultimately molt, particularly at colonies where local prey depletion forces individuals to forage far from the breeding site to recover from breeding.

Considering Ross Island colonies of which we have direct experience, Cape Crozier is almost entirely swept by frequent gale-force winds (leading to only a few molting penguins; some small piles of feathers are produced; Table 1). That contrasts with Cape Royds, which experiences the same winds but which has ample ridges behind which molting penguins can shelter (many molting penguins, relative to colony size; Figs. 3-5). In other parts of Antarctica, the provision of shelter has also been observed to be conducive to where penguins molt (Table 1; W. Fraser, pers. obs.). Among the various islands in Arthur Harbor, penguins breed on the windswept sides (winds blow away the snow to expose the gravel by which to build nests) but molt on the sheltered sides of the same islands (Cimino et al., 2025; M. Cimino, pers. comm.; W. Fraser, pers. obs.). The same factor operates even among penguins molting on sea ice --- the habitat required is compacted, multi-year ice, which tends to have large pressure ridges that shelter molting penguins (including emperor penguins (e.g. Cline et al., 1969; Ainley et al., 1984, 1998; Takahashi et al., 2018; W. Fraser, pers. obs.)). These ridges, whether on land or on sea ice, also lead to the accumulation of snowbanks (Fig. 3). While molting, the penguins constantly eat snow to maintain hydration (W. Fraser, pers. obs.). Many of the consistent molting locations near Palmer Station (Arthur Harbor) are where snow accumulates and often does not fully melt. Thus, snow is accessible in February (Cimino et al., 2025; M. Cimino, pers. comm.). The same is true of Royds.

4.2.2. Food availability. Another major factor affecting where Adélie penguins molt appears to be food availability. Penguins lose mass/condition during the breeding season, especially when foraging for chicks and themselves (Sapin-Jaloustre, 1960; Chappel et al., 1993; Ballard et al., 2010b). Therefore, after their chicks fledge, parents must forage sufficiently to recover condition as well as achieving a buffer to endure the two-three weeks of fasting needed for molt (and grow a new feather coat). During the molt, similar to what happens during breeding, Adélie

688 penguins lose 30-40% of their mass (Clark, 1906; Cedron, 1953; Sapin-Jaloustre, 1960; Penney,
689 1967). At locations such as Cape Crozier and Signy Island, where penguins are especially
690 numerous, colony residents, having depleted nearby prey, go elsewhere to regain condition and
691 remain to molt. Fortunately, pack ice is within a few hundred kilometers of the colony. Judging
692 from Crozier, where nearby prey is known to be significantly reduced by the large numbers of
693 central-based foraging penguins (Ainley et al., 2015), at the end of the breeding effort they have
694 to travel beyond the colony foraging area to find enough prey to fatten for the molt. They then
695 remain in the region where prey was abundant and try to find sea ice or another land site on
696 which to molt.
697
698 This scenario has been or is being tested in a long-term 'natural experiment' at Signy Island. As
699 noted in Table 1, during Sladen's (1958) field period, the population of Adélie penguins likely
700 was much higher than now, ~17,000 pairs, plus numbers of chinstraps were several times
701 higher, 35,000-55,000 pairs (Croxall et al. 1981). After breeding, Adélies apparently departed to
702 recover condition in the northwestern Weddell Sea pack ice where they remained to molt
703 (chinstraps stayed to molt on the island); this pattern and population size for Adelie penguins
704 continued into 2004 (Woehler et al., 2001; Dunn et al., 2011). Numbers of both species have
705 since decreased drastically, both now stand at ~1600 pairs (Forcada and Trathan, 2009; Dunn et
706 al., 2016). With lessened intra- and interspecific prey competition locally, at least some Adélie
707 penguins now stay to molt at Signy (P. Convey, pers. obs.; Table 1). In indirect support, there is
708 little evidence of penguin-depletion of prey at a location such as the small Cape Royds colony
709 (Ford et al., 2015; Ainley et al., 2018; Saenz et al., 2020), which could at least partially explain
710 why a relatively high proportion of penguins molt on or near the cape. Also, penguins from
711 other colonies arrive in the vicinity to fatten and remain to molt. Note that 60% of Adélie
712 penguin colonies are <10,000 pairs (data from Lynch and LaRue, 2014) and thus are candidates
713 for having elevated proportions of colony populations likely returning to molt (or in the
714 immediate vicinity).
715

This influx of penguins from other colonies was also noted by Penney (1967) at Windmill Islands. W. Fraser (pers. obs.), confirmed by P. Convey (pers. obs.), noted that the accumulation of molting penguins at Avian and Fish islands, Antarctic Peninsula, totaling perhaps 300,000 penguins (thus, exceeding the breeding population at those locations), appeared to be a response to incredibly rich food resources in the local fjords. This is also consistent with observations of molting Adelie penguins at other terrestrial locations (e.g., islands in Ryder Bay) relatively close to these colonies (P. Convey, pers. obs.) Submarine canyons, many of which lead into fjords, are rich in prey resources and appear to be a factor in determining where colonies occur (Santora et al., 2020). The location along the northern Victoria Land coast where many Adélie penguins molt (e.g. Capes Hallett and Adare), including 29% of Royds birds, is also associated with a submarine canyon: Drygalski Trench; Cape Royds and McMurdo Sound are at the south end of Drygalski Trench.

4.3 Limitations of the Study

Although most of the penguins molting at Cape Royds do so in the vicinity of the main breeding area, a significant number do not (as various accounts reveal). We had only one camera set-up but clearly if the goal was to have a view of all molting individuals, then 4-5 camera set-ups would be required. However, what we did have allowed us to document colony dynamics during molt at Cape Royds that previous researchers could not accomplish (they lacked the time and resources to remain into March). We doubt that the research situation at Cape Royds is unusual. Not many researchers, like Richard Penney (1967), managed to remain through the entire breeding and molting periods. While researchers over-wintered at Palmer Station during the 1960s, their need for a boat to visit molting areas was limited.

The other main limitation occurred because of the inclement weather that develops in the austral 'autumn.' There were repeated days when the molting birds could not be seen due to 'white outs' (blizzards) or the technology dealing with rapidly changing dew points etc --- fogging of the lenses. So, again, we had to do with the technology available, short of having

744 persons remaining through the entirety of molting period for 12 different breeding-molting
745 periods.
746
747 **5.0 CONCLUSIONS**
748
749 Although this study is not meant to imply that critical aspects of Adélie penguin life history are
750 not sea ice dependent, results suggest that some components such as the locations where this
751 species molts are less dependent on sea ice than previously thought. Such behavioral plasticity
752 may be underappreciated in this species but, as noted in the Introduction, it could be important
753 for understanding abiotic influences on this species' demographic adjustments to its highly
754 variable habitat.
755
756 A large portion of the censuses that we summarized from the literature involved just one year at
757 each site, and our time series at Cape Royds was only for 12 seasons. Obviously, a longer time
758 series would be preferred. We encourage researchers to pay more attention to molt. Despite
759 the limited examples, it appears that Adélie penguins are plastic in their choice of molting
760 habitat to an extent that has not been previously appreciated --- in some locations colony
761 members molt at the colony, in others only a portion does so, in a few none at all, and in some
762 many individuals from other colonies arrive to molt (colony or not; Table 1). In those sections of
763 Antarctic coast in which pack ice is within reach, Adélie penguins are more likely to molt in that
764 ice, in contrast to sections having no late summer sea ice.
765
766 Our analysis at Cape Royds further refines this understanding by showing that, over a 12-season
767 time series, regional sea-ice conditions and breeding population size are associated with
768 interannual variation in peak on-land molt counts. Higher January SIC and larger breeding
769 populations were both linked to fewer individuals molting on land, suggesting that
770 environmental context and reproductive status influence where molt takes place. This also hints
771 at the proposition that an appreciable number of penguins molting at Cape Royds are not from
772 that colony.

The Adélie penguin is among the most abundant of penguin species and has persisted through multiple glacial and interglacial periods, adapting to significant shifts in nesting habitat and sea ice. It is noteworthy that while other Antarctic penguins, such as the chinstrap and gentoo, generally avoid sea ice, Adélies and emperor penguins belong to a species group that consistently associates with it. The specific reasons for these differing habitat associations remain unknown. This divergence may be analogous to certain songbird species that associate with trees while others utilize adjacent brush or fields. The ecological success of the Adélie penguin is largely attributable to the plasticity of its life history strategies, including its approach to molting. The Adélie penguin is truly pagophilic but is not an ice-obligate species, as long thought. In the case of molt habitat, it is context-dependent, reflecting a high degree of behavioral and ecological plasticity.

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6.2 Author Contributions

Data acquisition: DGA, VM, GB, WF, PC, DA, RR; conception, writing and editing: DGA, VM, GB, WF, PC, DA, RR; data analysis: VM, GB, DGA.

6.3 Conflict of Interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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1034 Table 1. A summary, based on the literature, of information on the presence of molting Adélie
1035 penguins at various colonies and adjacent land/glacial areas during the molting period,
1036 February-March. Population estimates in italics from Woehler (1993 = W) or Antarctica NZ;
1037 otherwise, reference indicated.

Location	**Population (breeding pairs)**	**Date**	**Observation of molting**	**Source**
Ross Sea, south to north				
Cape Evans, 78 38S	Non-colony	1957	20-30 molting; nearest colony ~10 km north	Taylor, 1962 (Falla, pers. comm.)
Cape Barne, 78 00S	Non-colony	2000s	Extensive feather deposits; nearest colony ~1 km	S. Emslie, pers. comm.
Cape Royds, 77 30S	1200	1907-08	Fledglings depart from beach, old birds stay behind to molt	Murray, 1909
	2000	20 Feb, 1956	800 molting adults, including on the beach	Austin, 1957
	1400	14 Feb, 1960	540 adults, 3 yearlings;	Taylor, 1962
	~1500	4th week Feb 1964	~920, plus small numbers not in breeding area	Spellerberg, 1971
	1051	Feb 1965	387 in breeding area, 984 elsewhere	Yeates 1968
	2000-3000	2008-24	An average ~630 ± 150	This study
Black sand beach	Non-colony	2000s	Extensive feather deposits; ~1 km from colony	DGA, pers. obs.; S. Emslie, pers. comm.
Cape Crozier, 77 31S	100,000	Well into Feb, 1960-70s	few to none molt at the colony	Ainley et al., 1978
	102,000[a]	18 Feb, 1956	~1000	Austin, 1957
	150,000+	2000s	A few small deposits of feather; penguins tracked molted in the pack ice	S. Emslie, pers. comm.; G. Ballard, pers. obs.
Dunlop Is, 77 14S	Non-colony	2000s	Extensive feather deposits; nearest colony ~15 km	S. Emslie, pers. comm.

Cape Bird, 77 10S	*25,000-35,000 (W)*	1991 & 2000s	Perhaps low 100s molt; extensive feather deposits	Davis et al., 1996; L. Davis, pers. comm.; S. Emslie, pers. comm.
Beaufort Is, 76 56S		historic	Large feather deposits, from 45k years ago	Emslie et al., 2007; pers. comm.
Inexpressible Is, 74 54S	*11,000 (W)*	1911	Many adults molting	Levick, 1914
Edmonson Pt 74 20S	2000	2000s	Unknown, but large feather deposit	S. Olmastroni, pers. comm.
Cape Hallet, 72 19S	*43,000 (W)*	11 Feb, 1956	525-1295	Austin, 1957
	35,000 (W)	1997-98	Thousands molting	Davis et al., 2001; L. Davis, pers. comm.
	38,000 (W)	2001	Thousands, i.e. at least 5000, molting by 30 Jan	Nevins, 2001; pers. comm.
Cape Adare, 71 17S		17 Feb, 1899	"The majority of the Penguins have left now; those we saw were still in the moulting stage."	Hanson, 1902
		1904	Very large numbers molting	Wilson, 1907
		1910	Thousands molting	Levick, 1914
	240,000 in 1983 (W)	10 Feb, 1956	2,000 to 2,500 well-grown young and molting adults still present	Austin, 1957
East Antarctica, east to west				
Sabrina Island, 66 57S	*3471*	9 March, 1965	1500-2000, all in molt	Hatherton et al., 1965
Dumont d'Urville, 66 40S	*29,000 (W)*		"a limited proportion of penguins molt on the breeding areas"	Groscolas et al., 1986
	20,000-50,000	2015-20	Penguins tracked molted in pack ice	Zajková et al., 2025
Port Martin, 66 49S	50,000	1950	~15% of population molting	Sapin-Jaloustre, 1960
		3-11 March, 1951	About 60 adults molt in the colony, about 40 birds on a hill 1km from colony	Cendron, 1953
Windmill Is,	1,350	1958-60	307, one-fifth of colony	Penney, 1967

69 00S				
Béchervaise Is, 67 58S	1,800	1991-92	25% molting, though assessed before the peak	Kerry et al., 1993
Murray & Scullin Monolith, 67 47S	300,000 birds present	13 Feb, 1931	Half the population molting; other half feeding large chicks	Falla, 1937
Barrier Bay Polynya coast 67 45S	No colonies	1 March, 2012	Along 369 km of low coast, at 10 locations, groups (n = 16) averaged 38±26, range 8-101 molting penguins	B. Wienecke, pers. comm.
Hukuro Cove, 69 21S	150	2010	Penguins tracked molted in pack ice	Takahashi et al., 2018
Antarctic Peninsula, south to north				
Avian Is, 67 46S Rothera 67 34S	25,000	1976 1980-90s	More molting on land than size of breeding population No breeding colony, but molters present late Jan onwards on Rothera Point and local Ryder Bay islands, likely from Avian Island population; at other nearby colonies, e.g. Detaille Island, molting clearly takes place in largely ice-free areas	W. Fraser, pers. obs. P. Convey, pers. obs.
Fish Is, 66 01	15,000	1976	More molting on the island than size of breeding population	W. Fraser, pers. obs.
Argentine Islands 65 15S		19 Feb, 1948	A few molting	Sladen ,1958
Arthur Harbor 64 46S	20,000; 36,000 on Palmer Archipelago [b]	1960-80s	Entire population resident year- round, including molt	Parmelee, 1992; Chappell, 1993
	~1,000	1990-00s	Thousands once molted, but fewer as breeding population decreases --- as of recently to a few 100	W. Fraser, pers. obs.; M. Cimino, pers. comm.

Hope Bay, Antarctic Sound 63 23S	*120,000 (W)*	1949	A few yearlings molting	Sladen, 1958
Ardley Is 62 13S	*~65,000 in vicinity*	2020-21	Adults depart before molt	Zaldúa et al., 2024
Admiralty Bay 62 01S	15,000-18,000	1980-96	Adults depart before molt	Sierakowski et al., 2017
Scotia Sea				
Laurie Is 60 44S	*~100,000 (W)*	1904	Adults departed by 11 Feb, presumably to molt elsewhere	Clarke, 1906
Signy Is 60 43S	19,000[c]	1951	None molting	Sladen, 1958
	~20,000 [c]	1980s	Year-round resident; does leave when extensive sea ice forms but returns across sea ice very early season. Molts on island when little or no snow left.	P. Convey, pers. obs.
		2004	Molt in pack ice	Dunn et al., 2011
	~1600[d]	Jan-Feb, 2024	Large numbers molt along shore, vicinity of colonies	P. Convey, pers. obs;
South Sandwich Is 55-60 S	5 of 11 islands, 200 – 50,000	16 Jan-22 Feb, 1997	Populations on five islands. No specific 'molter' counts,' but they do so on land in vicinity of all the colonies	Convey et al., 1999; pers. obs.

[a] numbers in 1966 were 102,500 pair (Ainley et al., 1978)

[b] Poncet and Poncet (1987) for population size

[c] Croxall et al. (1981) for population size

[d] for population size: Forcada & Trathan (2009), Dunn et al. (2011, 2016)

Table 2. A summary of relevant values used in the analysis, including those from Supplementary Material Tables A1 and A2.

Year	Colony size[a]	Peak molt count[b]	Date peak	Last date	SIC 15 Jan	SIC all Jan	Ratio molt:colony size[c]	chicks/ pair
2008	1805	336	62	75	97.3	88.5	0.19	0.581
2009	2609	415	54	74	44.6	36.2	0.16	0.853
2010	2513	251	54	74	43.7	50.9	0.10	1.080
2012	3083	242	62	76	44.2	52.2	0.08	0.857
2013	2944	358	59	77	75.0	38.7	0.12	
2014	3187	233	62		51.3	47.7	0.07	0.796
2016	1746	75	64	77	90.5	91.6	0.04	0.348
2019	2513	158	53	75	33.8	37.4	0.06	0.320
2020	2582	300	51		13.8	11.5	0.12	0.799
2021	1967	590	59	76	43.5	50.8	0.30	0.780
2022	2209	153	61	76	91.9	67.0	0.07	0.806
2023	2298	542	60	69	38.4	39.6	0.24	0.939
2024	3168	126	61	77	29.3	27.8	0.04	1.070

[a]Occupied nests (pairs) on about 1 December each year; 2008-2016 estimate by counting aerial photos, 2019-2024 photos from an unmanned aerial vehicle.

[b]Number in camera viewscape, assumed to be 50% of the total molters (both camera views needed to reveal the total, so numbers in this column X two).

[c]Ratio was calculated by doubling number of pairs to determine breeding birds, doubling the maximum number of molting, and then dividing the latter by the former (see text). Therefore, the estimate does not include non-breeders, which might number the same as the count for breeding pairs (not breeding individuals). Hypothetically, the proportion of non- or failed breeders would be reflected in the chicks/pair (lower = more failed breeders).

Table 3. Effects of sea-ice concentration and colony size on peak on-land molt counts, based on a negative binomial generalized linear model (log link) explaining interannual variation in peak on-land molt counts of Adélie penguins at Cape Royds [a].

Predictor	Estimate (β)	SE	z value	p value
Intercept	21.91	8.15	2.69	0.007
Mean January SIC	**–0.022**	0.011	–2.06	**0.039**
Colony size (log breeding pairs)	**–1.94**	0.99	–1.96	**0.050**

Model details:

Negative binomial GLM (log link)

θ (dispersion parameter) = 4.63 ± 1.95

Residual deviance = 11.41 (df = 8)

[a] Colony size is expressed as the number of breeding pairs (log-transformed). Significance assessed using Wald tests; likelihood ratio tests are reported in the text Effect sizes are reported on the log scale. For SIC, estimates correspond to an approximate 2.2% decrease in peak on-land molt counts per 1% increase in mean January sea-ice concentration.

Figure Captions

Figure 1. McMurdo Sound, which lies between Victoria Land and Ross Island, and the location of Cape Royds showing the colony's typical foraging area, i.e. the 90% utilization distribution for Adélie penguins breeding at Cape Royds. Background imagery is MODIS Corrected Reflectance (Jan 13, 2016; True Color, 250 m resolution) from the NASA LANCE system (Collection 6.1), visualized via NASA Worldview. This foraging area was used to determine sea ice concentration in January, . determined during December-January 1997-2000 (4 summers) based on radio telemetry (Ainley et al. 2004), and during 2005-2007 (3 summers; Ford et al. 2015) as well as during 2012 (Saenz et al. 2020) based on SPLASH-tag satellite telemetry.

Figure 2. Cape Royds showing penguin subcolonies (shadings), position of Shackleton's Hut, and the two locations of the PCam (stars) and respective viewscapes, 2008-2010 and 2012-2024.

Figure 3. The anchored tower holding solar panels, control box, two cameras, weather instruments, and an iridium antenna deployed at Royds 2008-2024. The black box contains the batteries that are charged by the panels. Inset shows one of the cameras.

Figure 4. One of the five scenes of molting penguins provided daily, as the system panned left to right along the wind-protected ridge at Cape Royds. The Royal Society Range, on western shore of McMurdo Sound, visible in the background. Here ~52 penguins are sheltered in the lee of the ridge on a snow drift (25 February 2024). Snowdrifts, providing a water source, are characteristic of molt locations. The penguins leave a mat of guano and molted feathers, still present in the following spring. Tan-brown areas are of guano where penguins had nested earlier in the summer.

Figure 5. Daily tallies of molting penguins (A) in the lee of Shackleton's Hut; and (B) in the lee of a major ridge south of the Cape Royds colony (see Figs. 1, 4).

Figure 6. Predicted relationship between mean January SIC and peak on-land molt counts of Adélie penguins at Cape Royds, based on a negative binomial generalized linear model including

sea ice and colony size (held at its mean). The solid line shows the fitted relationship, and the shaded area indicates 95% confidence intervals.