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Biological Sciences

Divergent responses of *Pygoscelis* penguins to unfavourable weather conditions in the South Shetland Islands

Ana Laura Machado-Gaye[1], Gaston Manta[1], Christina Braun[2], Javier Menéndez-Blázquez[3], Maryam Raslan[1], Natalia Zaldúa[1,4] and Álvaro Soutullo[1]

[1]Centro Universitario Regional del Este, Universidad de la República, Maldonado, Uruguay; [2]Polar & Bird Ecology Group, Institute of Ecology and Evolution, University of Jena, Jena, Germany; [3]Instituto Cavanilles de Biodiversidad y Biología Evolutiva (ICBiBe), Universitat de València, Paterna, Spain and [4]Vida Silvestre, Uruguay

Abstract

Pygoscelis penguins are valuable indicators of the effects of rapid warming in the Antarctic Peninsula. In the western Antarctic Peninsula, Adélie penguins show a declining population trend, whereas gentoo penguins are expanding. The notably low reproductive success of Adélie but not gentoo penguins at Ardley Island during the 2023/2024 breeding season provided an opportunity to explore the potential effects of weather conditions and food availability as possible determinants of reproductive output. We explore associations between reproductive output, air temperature, wind speed, wind chill temperature and accumulated rain and snow. As a proxy for food availability, we used data of penguins' foraging trips, which reflect krill abundance. A late-winter storm at the end of October 2023 led to a record-low wind chill temperature and sustained snow cover, negatively affecting the number of eggs that hatched successfully and/or the number of chicks that survived the first days after hatching. The effects were similar for both species, yet for gentoo penguins chick survival in the late stage of the chick-rearing phase was remarkably higher, possibly due to high food availability and a longer nestling period. As previously suggested, the greater plasticity of gentoo penguins may allow them to mitigate the negative effects of environmental variability, potentially explaining this divergent breeding success despite unusually harsh meteorological conditions.

Keywords: Breeding phenology; foraging trips; King George Island; *Pygoscelis adeliae*; *Pygoscelis papua*

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Introduction

Antarctic Peninsula warming in the late twentieth century was greater than anywhere else in the Southern Hemisphere (Turner *et al.* 2005, Siegert *et al.* 2019). The surrounding waters of the Southern Ocean have become warmer and fresher, resulting in changes in oceanic circulation (e.g. Armour *et al.* 2016, Haumann *et al.* 2016, Pellichero *et al.* 2017, Chown *et al.* 2022), changes in the duration and extent of sea ice (e.g. Comiso *et al.* 2017) and acceleration of the breaking of ice shelves (e.g. Liu *et al.* 2015). Under a 1.5°C global warming scenario, Antarctic Peninsula temperatures are expected to increase by 1–2°C in winter and 0.5–1.0°C in summer, with up to 130 days per year above 0°C, leading to increased rain, snow and ice melt and surface run-off (Siegert *et al.* 2019). Sea-ice extent is expected to be highly variable in the Western Antarctic Peninsula (WAP), and southwards shifts in marine life distributions are expected to continue (Atkinson *et al.* 2019). The WAP is also one of the regions in Antarctica with the highest human footprint (Pertierra *et al.* 2017), mostly because of the accumulation of research and logistical infrastructures and the concentration of touristic activities and krill fisheries (Hogg *et al.* 2020).

All these changes have noticeable impacts on diverse biological processes (Ducklow *et al.* 2007, McClintock *et al.* 2008, Convey & Peck 2019, Schofield *et al.* 2024). However, understanding and predicting biological responses is complex, as they may occur at all trophic levels and vary according to different regional or local conditions (Clarke *et al.* 2007, Trathan *et al.* 2007, Rogers *et al.* 2020). *Pygoscelis* penguins are often considered valuable indicators of the impacts of these changes on Antarctic ecological communities (Ainley 2002, Boersma 2008). Particularly interesting are the sympatric populations of the three *Pygoscelis* species across the WAP, which are already showing contrasting trends in response to climate change impacts in this region. Overall, while Adélie penguins (*Pygoscelis adeliae*) and chinstrap penguins (*Pygoscelis antarctica*) show a decreasing trend in population size, gentoo penguins (*Pygoscelis papua*) are expanding both in number and spatial extent (Lynch *et al.* 2012, Herman *et al.* 2020).

Human- and climate-induced changes may have differential effects on *Pygoscelis* penguins depending on their life-history strategies. Population size fluctuations have been linked to breeding success, the survival rate of adults or juveniles and factors operating both at a local scale during the breeding season (e.g. prey availability or competence with other species or fisheries) and at a larger scale during the non-breeding season (e.g. sea-ice extent

Corresponding author: Ana Laura Machado-Gaye; Email: almachado90@gmail.com
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in winter, krill recruitment; Hinke *et al.* 2007, Carlini *et al.* 2009, Cimino *et al.* 2023, Salmerón *et al.* 2023). In general, the population decline of Adélie and chinstrap penguins has been closely related to large-scale changes in the biomass of Antarctic krill, their main prey. In contrast, gentoo penguins are considered to have more generalist foraging strategies and a flexible trophic niche, although they also predominantly feed on krill during the summer in the WAP (Polito *et al.* 2015, Herman *et al.* 2017, McMahon *et al.* 2019). Additionally, migration during non-breeding months has been proposed to be an important factor in the population trends of these species. Gentoo penguins are a non-migratory species and remain close to their breeding colonies during the winter, allowing them to assess local environmental conditions at the breeding site and thus achieve greater flexibility in adjusting to these conditions (Hinke *et al.* 2012, Juáres *et al.* 2013, Korczak-Abshire *et al.* 2021). In contrast, Adélie and chinstrap penguins migrate long distances to their wintering habitats, which precludes adequate phenological responses to changing local conditions at breeding sites (Hinke *et al.* 2012, Zaldúa *et al.* 2024).

However, although most of the research in the WAP has focused on the potential effect on population trends of prey availability during the summer season (due to differences in penguins' trophic niche and dietary flexibility; Hinke *et al.* 2007, Trivelpiece *et al.* 2011, Juáres *et al.* 2013, Cimino *et al.* 2016, Salmerón *et al.* 2023), other factors, such as the effects of weather conditions on breeding success, have been studied only at a limited number of colonies. These studies have shown that local weather conditions may directly influence the timing of reproduction in penguins, brood survival and chick mass at fledging (Lynch *et al.* 2009, 2012, Hinke *et al.* 2012, Fraser *et al.* 2013, Cimino *et al.* 2014, Juáres *et al.* 2015). For example, it has been suggested that cold spring air and severe snowstorms that prevent snowmelt at the beginning of the breeding season can delay clutch initiation dates, given the need for these species to find snow-free areas for nest building (Hinke *et al.* 2012, Lynch *et al.* 2012, Cimino *et al.* 2019). The accumulation of snow may also cause early nest desertion or reduce the survival of eggs or chicks due to nest flooding (Trivelpiece & Fraser 1996, Cimino *et al.* 2014, Juáres *et al.* 2015). Precipitation, strong winds and low air temperatures during critical periods such as hatching may also be factors in reducing chick survival, as new hatchlings and young chicks are ectothermic and are particularly vulnerable to hypothermia during this period (Moreno *et al.* 1995, Olmastroni *et al.* 2004, Demongin *et al.* 2010, Chapman *et al.* 2011, Smiley & Emmerson 2016).

Recently, Salmerón *et al.* (2023) proposed that a combination of low sea ice in winter and weather conditions during spring and summer have significant impacts on krill abundance and, as a consequence of limited food availability, on the breeding success of chinstrap penguins breeding in the South Shetland Islands region. In contrast, Machado-Gaye *et al.* (2025) did not find differences in breeding success of Adélie penguins between years during the same period and in the area. Scarcity in food availability was, however, reflected in the foraging behaviour of both species, with them embarking on longer foraging trips during the chick-rearing stage in years with low krill abundance (Salmerón *et al.* 2023, Machado-Gaye *et al.* 2024, 2025). Therefore, the observations of extremely low reproductive success in Adélie but not gentoo penguins in the colonies of Ardley Island (King George Island) during the 2023/2024 breeding season provide a unique opportunity to explore the relative contributions of the effects of weather conditions and prey abundance on the breeding success of these colonies.

To identify putative determinants of this low reproductive success, here we explore associations between the breeding output of the two species during five breeding seasons (2019/2020–2023/2024) and a set of weather conditions that have been suggested as potential determinants of egg failure or chick mortality. Specifically, we explore potential links with i) air temperature, ii) wind speed, iii) wind chill, iv) rain and v) snow cover in the area during October–December (the incubation and chick-rearing stages in Ardley Island). We also explore associations with characteristics of their foraging trips as indicators of food availability. By integrating data on adult foraging behaviour, chick survival rates throughout the chick-rearing stage and weather conditions, we aim to identify the ecological mechanisms underlying the unusual and contrasting breeding outputs observed during 2023/2024. We specifically explore the following alternative hypotheses: 1) higher snow accumulation at the beginning of the breeding season (November) decreased egg success and/or hatchling survival due to eggs freezing/cracking or chick hypothermia caused by nest flooding (late November/early December), 2) higher wind intensity and lower air temperature (low wind chill) and higher rainfall during the chick-rearing period (December) decreased chick survival due to hypothermia, and 3) reduced food availability during the chick-rearing period decreased the amount of food delivered to the chicks, causing higher mortality due to starvation.

Methods

Study area

Field studies were conducted from November to February in Ardley Island (62°13′S, 58°56′W), in the south-west of King George Island/Isla 25 de Mayo, South Shetland Islands, an Antarctic Specially Protected Area (ASPA N°150), during five breeding seasons (2019/2020–2023/2024; Fig. 1). This colony is one of the few sites where Adélie, gentoo and chinstrap penguins breed sympatrically (Braun *et al.* 2017). The colony holds special importance for gentoo penguins, as > 1% of the global population nests there (Braun *et al.* 2017, Donald *et al.* 2019). Consequently, the terrestrial area is designated as Important Bird Area (IBA) No. 48, and part of the surrounding marine area is recognized as marine IBA No. 11 (BirdLife International 2024). Since 2019, the Ardley Island colony is also a designated site under the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) Ecosystem Monitoring Program (CEMP). Breeding population size has been monitored since the 1980s for the three penguin species present there. According to Braun *et al.* (2017), the number of breeding pairs of chinstrap penguins has declined by more than 90% since the 1980s. However, this decline occurred mainly during that decade, when the population dropped from ~240 to fewer than 20 nests, remaining relatively stable thereafter. In contrast, Adélie penguins exhibited marked variability from the 1970s to the 1990s, followed by a sharp decline in the early 2000s, and a further decrease to < 200 nests between 2018 and 2022. In contrast, gentoo penguins increased over the same period by more than 80% (Humphries *et al.* 2017).

Breeding parameters

Following the standard methods of CCAMLR (2014), we defined reproductive success based on three counts conducted in different stages of the breeding seasons (Method A6C): 1) the number of nests with eggs, 2) the number of nests with chicks when hatching

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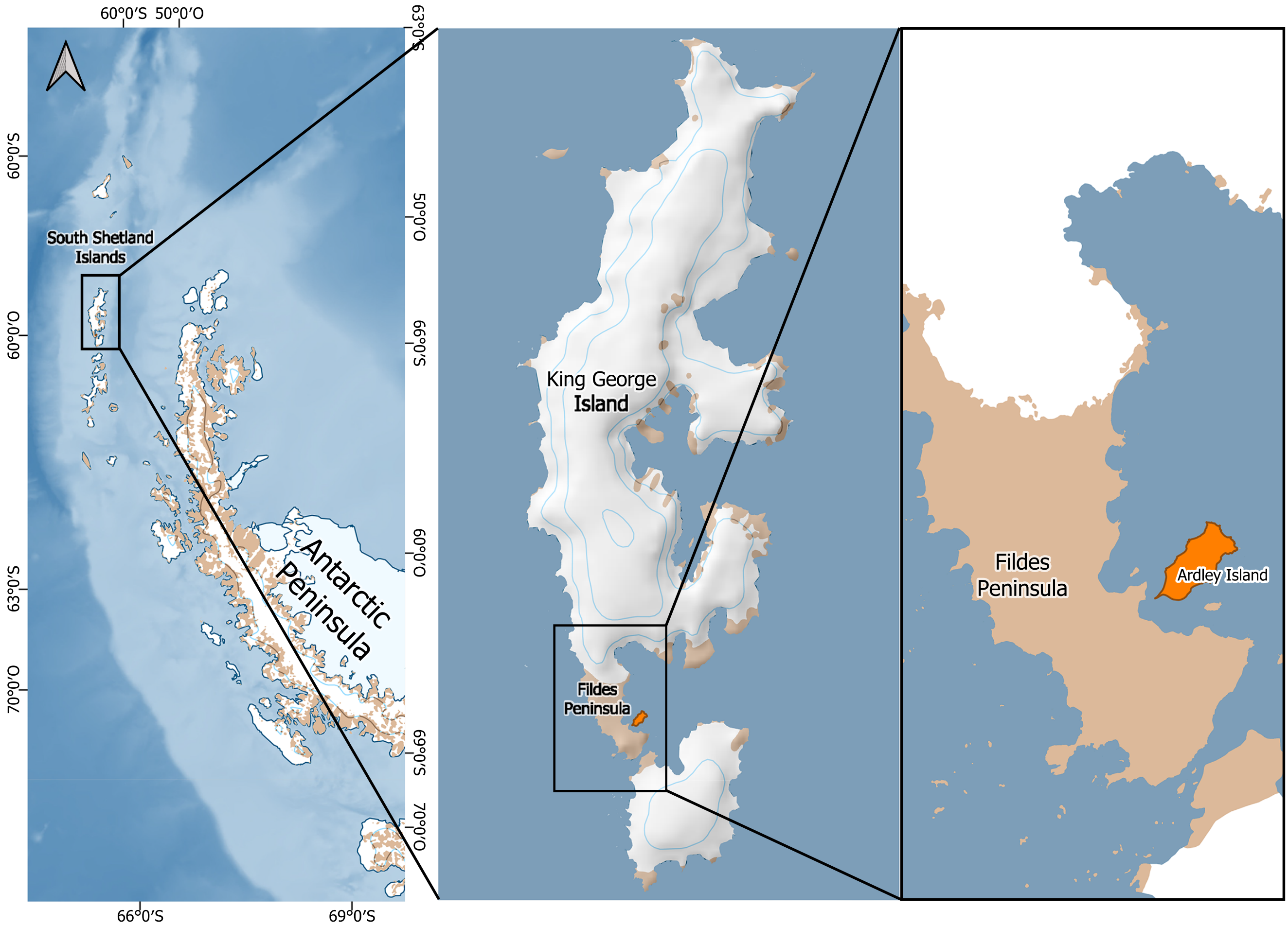

Figure 1. Location of Ardley Island colony on King George Island/Isla 25 de Mayo, South Shetland Islands, Antarctica.

was complete and 3) the number of chicks in crèche. For each count, three separate counts on the same day were performed by independent researchers for the entire colony of Adélie and gentoo penguins, and mean values were calculated (Table I). The mass of fledgling chicks of gentoo penguins was measured during three periods of 5 days in duration each following the CCAMLR protocol Method A7A (CCAMLR 2014; i.e. chick weight was measured in three consecutive periods of 5 days in duration each, with the first period beginning when the first fledglings appear on the beach). This enables the recording of differences in weight of early *vs* late fledglings. Fledgling chicks of Adélie penguins were weighed on a single day once they left their natal colonies and were on the beach (CCAMLR protocol Method A7B; CCAMLR 2014). It is worth noting that, as the Adélie penguin colony on Ardley Island is very small, fledglings depart within a narrow window of only 1–2 days, which often limits the possibility of conducting timely weight measurements. During this period, chicks of both species were captured near the water with a long-handled net and weighed with spring scales to the nearest 50 g. Only Adélie and gentoo penguins were considered in this study due to the low number of chinstrap penguin breeding pairs on Ardley Island. Due to logistical limitations (including those due to the COVID-19 pandemic), not all stages could be sampled equally in the 5 years of the study.

We calculated three indices of breeding success to account for variations in each stage throughout the season. For each season we calculated: 1) breeding success (number of chicks in crèche divided by the number of nests with eggs), 2) proportion of hatched nests (number of nests with chicks divided by the number of nests with eggs) and 3) hatchling survival (number of chicks in crèche divided by the number of nests with chicks).

Penguin foraging characteristics

During the five breeding seasons, 88 Adélie and 101 gentoo penguin adults rearing chicks were equipped with data-loggers (Axy-Trek, 70 × 40 × 15 mm, 69 g; TechnoSmart, Italy). Recorders were attached to only one member of the pair in nests with two chicks using black Tesa® 4651 tape (Wilson *et al.* 1997). The tagged birds were recaptured in the nest after 3–8 days and the loggers were removed to access recorded data. From 189 deployments, we obtained 839 complete foraging trips, and we analysed these data using *R* software (version 4.1.3; R Core Team 2022). Excess points recorded at departure and arrival were manually removed, retaining five points at the colony for each event. A speed filter was applied to remove unrealistic velocities (> 7 km h^{-1} for Adélie penguins and > 10 km h^{-1} for gentoo penguins). Foraging trips were defined from the time the birds moved more than 50 m from the nest to the sea until the time they were within 50 m of the nest again. For each individual, we calculated total trip duration, total trip distance (as the cumulative horizontal distance between all GPS locations per bird per trip) and maximum distance to the colony (as the straight-line distance between the colony and the

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Table I. Measures of breeding parameters of Adélie and gentoo penguins breeding in Ardley Island (King George Island/Isla 25 de Mayo) during five breeding seasons (2019/2020–2023/2024).

Breeding parameter	2019/2020	2020/2021	2021/2022	2022/2023	2023/2024
Adélie penguins					
Nests with eggs (*n*)	303	-	202	184	209
Nests with chicks (*n*)	262	353	162	168	129
Chicks in crèche (*n*)	350	408	224	235	163
Breeding success (chicks in crèche/nests with eggs)	1.16	-	1.11	1.28	0.78
Proportion of hatched nests (nests with chicks/nests with eggs)	0.86	-	0.80	0.91	0.62
Hatchling survival (chicks in crèche/nests with chicks)	1.34	1.16	1.38	1.40	1.26
Chick mass at fledging (g)	-	2905 ± 402	2800 ± 465	3700 ± 449	3780 ± 390
		(*n* = 79)	(*n* = 14)	(*n* = 80)	(*n* = 22)
Gentoo penguins					
Nest with eggs (*n*)	6695	-	7083	-	7846
Nest with chicks (*n*)	5768	6107	-	8763	5255
Chicks in crèche (*n*)	8903	7720	7906	8914	9650
Breeding success (chicks in crèche/nests with eggs)	1.33	-	1.12	-	1.23
Proportion of hatched nests (nests with chicks/nests with eggs)	0.86	-	-	-	0.67
Hatchling survival (chicks in crèche/nests with chicks)	1.54	1.26	-	1.02	1.84
Chick mass at fledging (g)	5183 ± 189	4151 ± 211	4785 ± 240	4900 ± 554	5070 ± 540
	(*n* = 120)	(*n* = 300)	(*n* = 280)	(*n* = 260)	(*n* = 270)

Note: '-' indicates unavailable data.

furthest point of a trip). Further details on field procedures and location analyses are provided in Machado-Gaye *et al.* (2024) and Soutullo *et al.* (2024).

Meteorological data

To describe weather conditions in the colony, we used *in situ*-measured meteorological data at the Chilean Frei Station at King George Island, ~4 km from the study colonies, between 1994 and 2023, covering a 30 year period. The variables used were daily values of mean temperature, accumulated rainfall and mean wind speed. Accumulated snow was also used, but these data are only available since 2012. Wind chill was calculated using air temperature and wind speed, following Osczevski & Bluestein (2005). Anomalies were calculated by subtracting the mean value of the respective day or month in the 30 year period. Finally, National Center for Environmental Prediction/ National Center for Atmospheric Research (NCEP/NCAR) re-analysis data (Kalnay *et al.* 1996) were used to study the large-scale weather situation that generated a 30 year record-low wind chill anomaly at Frei Station during the penguin breeding season (October–December) on 28 October 2023.

Statistical analyses

Variation in breeding success, proportion of hatched nests and hatchling survival between seasons were evaluated using χ^2 tests. To test for differences in foraging trip characteristics between seasons, we used linear mixed models (LMMs) implemented in the *R* package *lme4* (Bates *et al.* 2015). For each model, a residual analysis was performed to test the homoscedasticity and normality of the residuals. As the variables analysed for Adélie penguins did not present a normal distribution, they were log-transformed. Season was considered an independent factor variable and individual (ID) a random effect to account for repeated measures of the same individual. For the variable that did not have repeated measures by individual (fledgling body mass), we used a one-way analysis of variance (ANOVA), with the season as a factor. When significant differences between seasons were detected, we performed *post-hoc* Tukey tests using the *multcomp* package (Hothorn *et al.* 2008).

To test alternative hypotheses that could explain the observed low breeding success in Adélie penguins but not in gentoo penguins during the 2023/2024 breeding season, we conducted a series of analyses. First, we identified whether November 2023 had high accumulated snowfall for the study period by ranking the accumulated values for each year throughout the 30 years with weather data. Second, we examined whether, during December 2023, wind intensity was higher, air temperature was lower and, as a consequence, wind chill was lower, or whether accumulated rainfall was greater compared to other seasons, also using a comparative ranking of mean/accumulated values. Finally, we analysed foraging behaviour data to determine whether the duration, total distance or maximum distance of foraging trips differed significantly in 2023/2024 relative to the other years with tracking data.

Finally, to explore the relationship between breeding success and weather conditions, we performed a principal coordinates analysis (PCoA) based on the meteorological variables included in Hypotheses 1 and 2 (i.e. snow accumulation in November; wind speed, air temperature, wind chill and rainfall in December). Study years were ordered according to their position along the two main PCoA axes, providing a composite gradient of environmental severity to assess potential associations with breeding outcomes.

Results

Breeding parameters

Although we acknowledge that there are gaps in some variables and years, we observed that the breeding population of Adélie penguins on Ardley Island declined by more than 30% during the study period. In contrast, gentoo penguin breeding pairs increased by 17% (Table I). Throughout the 5 years of this study, significant differences were found in the breeding success of both Adélie penguins (χ^2 = 13.51, df = 3, P = 0.003) and gentoo penguins (χ^2 = 157.01, df = 2, P < 0.001), with 2023/2024 being the year with the lowest breeding success for Adélie penguins but not for gentoo penguins (Table I). For both species, we also found significant differences in the number of nests with eggs that hatched successfully and had chicks that survived the first few days after hatching (χ^2 = 7.78, df = 3, P = 0.05 and χ^2 = 99.12, df = 1, P < 0.001 for Adélie and gentoo penguins, respectively). In particular, we observed that the 2023/2024 breeding season had the highest rate of egg failure at hatching and/or hatchling mortality for both species (Table I). In contrast, survival rate of chicks to crèche did not show significant differences between seasons for Adélie penguins (χ^2 = 3.58, df = 4, P = 0.5), whereas for gentoo penguins the maximum value recorded for the study period occurred in 2023/2024 (χ^2 = 758.69, df = 3, P < 0.001). In summary, our results showed that the 2023/2024 season had the lowest hatching and early chick survival rates, as well as the lowest overall breeding success for Adélie penguins, whereas in gentoo penguins only hatching and/or early chick survival were reduced. The weight of fledglings varied significantly during the study period for both Adélie penguins (ANOVA: F = 36.79, P < 0.001) and gentoo penguins (ANOVA: F = 137.7, P < 0.001), with 2023/2024 being the season in which the highest chick mass was recorded for Adélie penguins and the second highest was recorded for gentoo penguins (Table I). Although sample sizes were relatively small in some seasons for Adélie penguins, they represent a substantial proportion of the colony's fledglings. However, these results should still be interpreted with due caution.

Penguin foraging characteristics

Our dataset consisted of 345 trips for Adélie penguins and 494 trips for gentoo penguins (Table II). Over the five seasons of study, Adélie penguins exhibited significant differences in their foraging trip characteristics. We found significant differences in foraging trip duration (LMM: F = 16.26, P < 0.0001), maximum distance (LMM: F = 11.19, P < 0.0001) and total distance travelled (LMM: F = 14.93, P < 0.0001) in the 2019/2020 and 2023/2024 seasons compared to the other seasons, but no significant differences were found between 2019/2020 and 2023/2024. During these two seasons, the lowest values for the three parameters were recorded, suggesting high food availability (Fig. 2a). Foraging trip characteristics of gentoo penguins showed slight variations between seasons (Fig. 2b). Trip duration during 2019/2020 did not differ significantly from that of summer 2023/2024, although it did significantly differ from those of other seasons (LMM: F = 4.43, P < 0.01). Regarding maximum and total distance, trips made by gentoo penguins during 2019/2020 and 2023/2024 showed the lowest values, with significant differences compared to the 2020/2021 season (LMM: F = 3.01, P < 0.05; LMM: F = 2.93, P < 0.05, respectively).

Meteorological conditions during the breeding seasons

Meteorological data from the Chilean Weather Service at Frei Station showed large seasonal and interannual variability. Accumulated snow shows a clear seasonal cycle, decreasing from 77 ± 66 cm in October to 41 ± 31 cm in November and 17 ± 17 cm in December, and rainfall follows a similar pattern, decreasing from 53 ± 45 mm to 43 ± 24 mm and 35 ± 19 mm, respectively. These patterns coincide with increasing temperatures as the season progresses. While air temperature and wind chill are primarily driven by the seasonal cycle, wind speed is influenced mainly by high-frequency variability (Fig. 3).

Meteorological data during the 5 years with overlapping penguin data (October–December 2019–2023) showed large season-to-season variability, registering both seasons with values close

Table II. Summary of the foraging trips (mean ± SD) of Adélie and gentoo penguins breeding in Ardley Island (King George Island/Isla 25 de Mayo) during five breeding seasons (2019/2020–2023/2024). For each season the following parameters are shown: total number of trips, number of individuals tracked, trip duration (h), maximum distance from colony (km) and total distance travelled (km).

Parameters	2019/2020	2020/2021	2021/2022	2022/2023	2023/2024
Gentoo penguins					
Trips (n)	100	83	115	122	74
Individuals (n)	19	20	21	21	8
Trip duration (h)	9.39 ± 3.31	11.94 ± 4.26	12.07 ± 4.41	12.09 ± 4.84	10.85 ± 3.41
Maximum distance (km)	16.54 ± 9.85	22.85 ± 11.55	18.55 ± 10.89	17.48 ± 11.32	15.43 ± 10.32
Total distance (km)	38.07 ± 19.89	51.97 ± 24.40	44.80 ± 23.28	42.10 ± 26.07	36.79 ± 21.03
Adélie penguins					
Trips (n)	67	59	98	86	35
Individuals (n)	19	16	24	10	6
Trip duration (h)	9.07 ± 4.67	20.85 ± 11.01	19.31 ± 10.98	16.73 ± 11.11	10.92 ± 6.28
Maximum distance (km)	6.60 ± 5.42	25.15 ± 17.92	16.95 ± 16.30	19.25 ± 16.95	10.30 ± 11.67
Total distance (km)	19.33 ± 12.33	64.66 ± 40.39	46.95 ± 37.94	47.80 ± 41.21	25.43 ± 27.00

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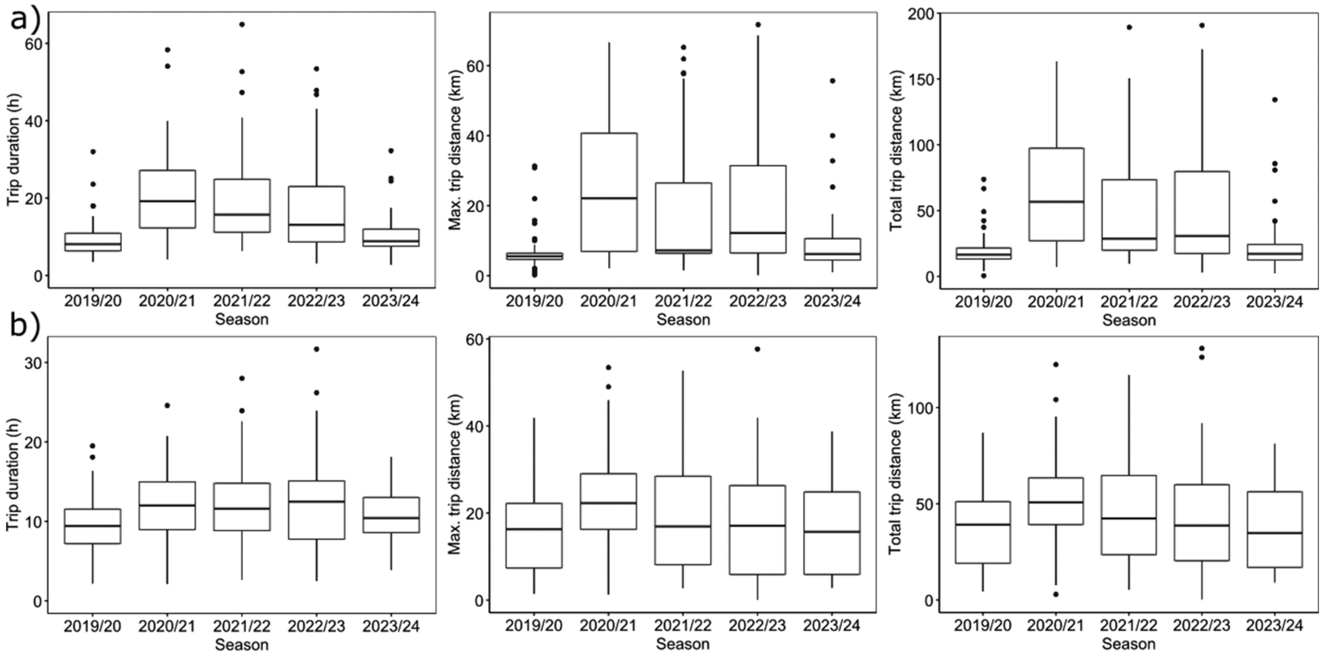

Figure 2. Foraging trips characteristics of **a.** Adélie penguins and **b.** gentoo penguins breeding in Ardley Island (King George Island/Isla 25 de Mayo) between the 2019/2020 and 2023/2024 seasons.

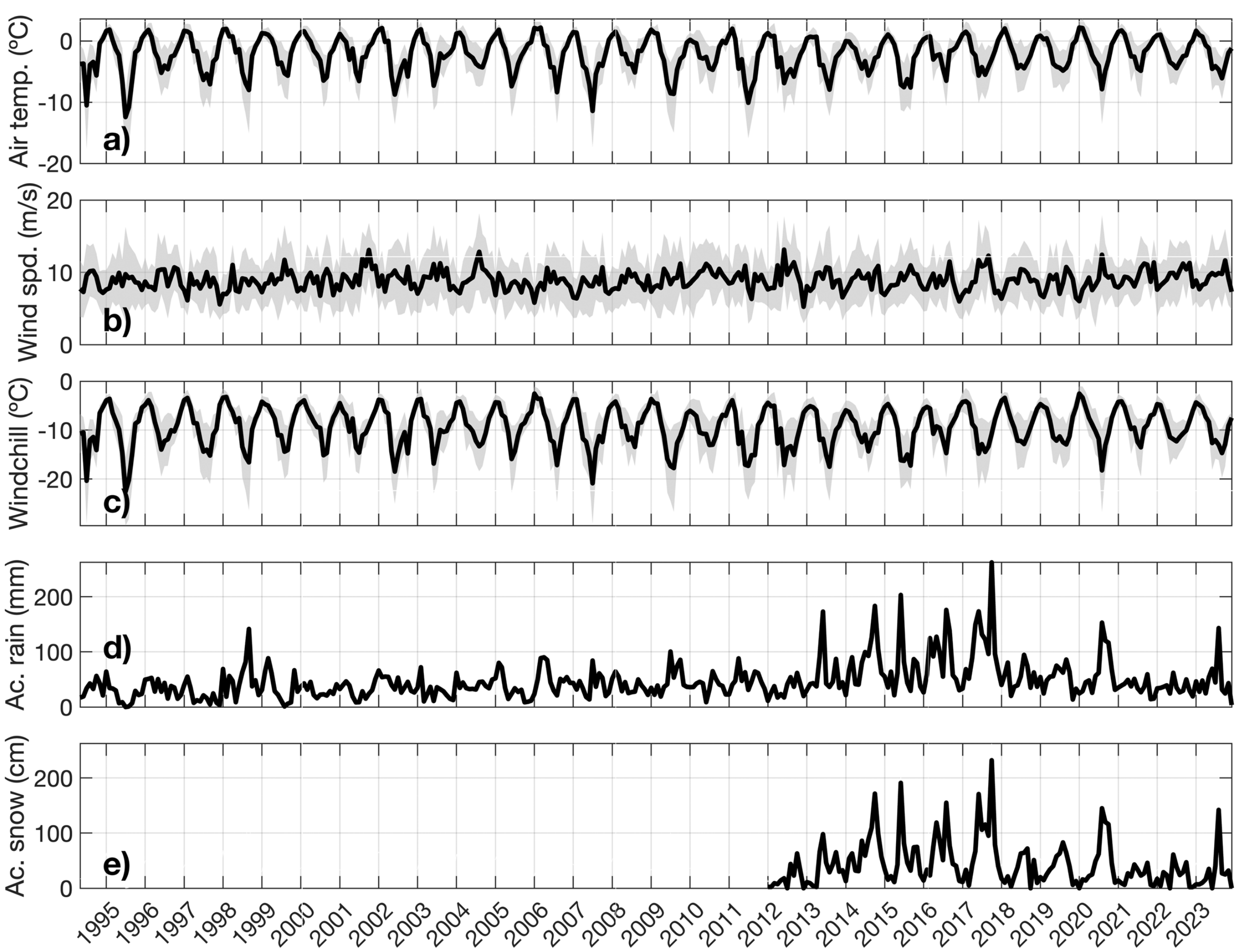

Figure 3. 30 years of *in situ* meteorological conditions at Frei Station on King George Island between 1994 and 2023. Black lines show monthly means of **a.** air temperature (°C), **b.** wind speed (m/s), **c.** wind chill (°C), **d.** accumulated rain (mm) and **e.** accumulated snow (cm). Panels **a.**, **b.** and **c.** also show the standard deviations of the variables as grey shading.

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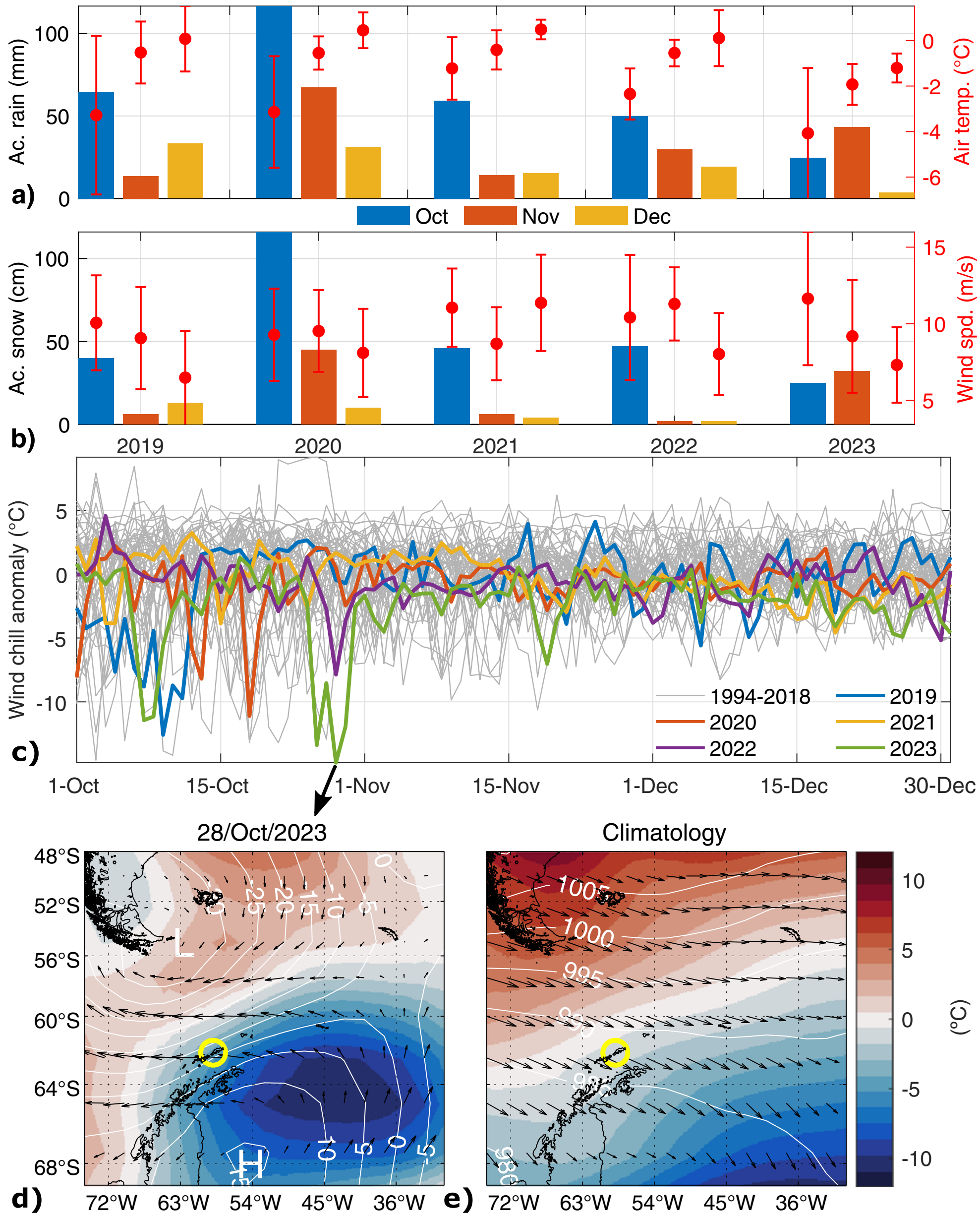

Figure 4. Meteorological conditions at King George Island during the breeding seasons of 2019/2020–2023/2024. **a.** Monthly accumulated rain (mm; bars) and mean air temperature (°C; dots). **b.** Monthly accumulated snow (cm; bars) and mean wind speed (m/s; dots) at Frei meteorological station for October, November and December between 2019 and 2023. **c.** Daily average of wind chill temperature (°C) at Frei meteorological station for October, November and December between 2019 and 2023. **d. & e.** Composites of 10 m mean wind (m/s; black vectors), mean sea-level pressure (hPa; white contours) and 2 m air temperature anomalies (shading) for the National Center for Environmental Prediction/National Center for Atmospheric Research (NCEP/NCAR) re-analysis in the Antarctic Peninsula for **d.** 28 October 2023 and **e.** climatology. The yellow circles show the location of the study site.

to the 30 year average such as 2022 and very anomalous seasons such as 2021 and 2023. In particular, 2023 was the coldest season as well as the season with the greatest wind chill. October 2023 recorded the second highest average wind speed and the third lowest wind chill temperature for any October in the 30 year record. November 2023 recorded the highest accumulation of snow and rain among all Novembers with breeding data, excluding 2020, which had higher values, but for that year breeding output data are not available as the island was inaccessible due to COVID-19 restrictions. December 2023 was the driest in the 30 year period, with the second lowest wind chill and the third coldest air temperature on record (Table S1).

During most days across all breeding seasons, wind chill temperatures remained above −15°C (Fig. 4c). Temperatures below −15°C were only recorded during Octobers. Of the three events during which wind chill dropped below −20°C during the 5 years with overlapping breeding data, two occurred in 2023 and one occurred in 2019. The sharpest decline in wind chill was observed on 28 October 2023, primarily due to an anomalous low-pressure system in the Drake Passage (marked with 'L' in Fig. 4d) and a relatively high-pressure system centred in the Weddell Sea that brought strong, cold south-easterly winds to Ardley Island. This weather pattern was also observed during the other extreme wind chill events. The date of 28 October 2023 marked the lowest wind

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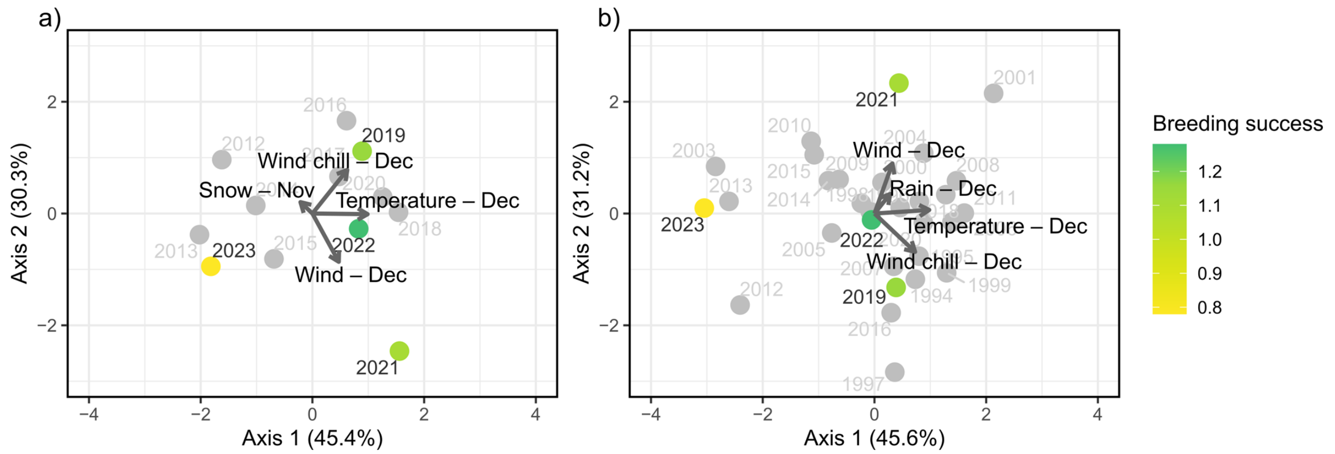

Figure 5. Principal coordinates analysis (PCoA) of meteorological variables and breeding success. Breeding success of Adélie penguins is shown as an example. **a.** PCoA of meteorological variables for the period 2012–2023 (temperature, wind, wind chill and snow) and **b.** PCoA including meteorological variables for the period 1994–2023 (temperature, wind, wind chill and rain).

chill anomaly (−14.77°C, indicated by an arrow in Fig. 4c) in the 30 years analysed at Frei meteorological station, which corresponds with an absolute value of wind chill of −23.4°C. NCEP reanalysis shows that King George Island experienced a reverse in the prevalent westerly winds, with velocities up to 18 m/s, due to a very-low-pressure system centred on the Drake Passage, producing an advection of very cold air from the Weddell Sea, dropping temperatures 8°C below the expected climatological values on 28 October 2023 (Fig. 4d,e).

PCoA was performed to explore the inter-annual variability of weather conditions and their possible relationship with Adélie penguin breeding success, and it showed that 2023 was an anomalous year in which, in addition to December temperature, wind and windchill, November accumulated snow and December rainfall were also considered (Fig. 5). This analysis also showed that the lowest breeding success coincided with years that experienced extreme weather conditions, especially 2023.

Discussion

The main drivers of population changes in *Pygoscelis* penguins in the WAP have been widely debated. Overall, the differential ability of these species to adapt their breeding chronology to local conditions, the availability of prey during the breeding season and overwintering factors affecting the survival of juveniles and adults have been the main proposed modulating factors (Hinke *et al.* 2007, 2012, Emmerson *et al.* 2011, Lynch *et al.* 2012, Juáres *et al.* 2013, Cimino *et al.* 2016). Our results, combining data on the population parameters of Adélie and gentoo penguins nesting on Ardley Island and the characteristics of their foraging trips over five breeding seasons, add evidence to the reports on the differential responses of these species to meteorological conditions during breeding seasons in the WAP. In particular, our observations strongly support the hypothesis that unusual weather conditions during the early breeding season may have a significant impact on the population trends of Adelie penguins in the WAP, irrespective of food availability.

Weather conditions at the beginning of the breeding season, specifically mean October temperatures and snow accumulation at nest sites, have been proposed as relevant factors affecting breeding success (Lynch *et al.* 2009, 2012, Hinke *et al.* 2012, Juáres *et al.* 2013). The main mechanism proposed to explain this process is that increased snow accumulation and low temperatures that prevent early melting may lead to loss of breeding habitat early in the season, as well as increased egg failure and loss of chicks due to late melting soaking chicks, leading to hypothermia. In eastern Antarctica, it has been reported that the peak of Adélie penguin nest failure occurs in the first few days after hatching, as chicks do not yet fully regulate their body temperature, being especially vulnerable to unfavourable environmental conditions (Olmastroni *et al.* 2004, Smiley & Emmerson 2016). Conversely, for gentoo penguins it has been suggested that the increased ability to alter their breeding chronology by delaying the timing of egg-laying under unfavourable local conditions, or even re-laying after early failures of nests, allows them to buffer impacts on their reproductive success under changing conditions (Lynch *et al.* 2009, 2012, Hinke *et al.* 2012, Juáres *et al.* 2015). On Ardley Island, during the 2023/2024 season we observed the lowest breeding success for Adélie penguins over the 5 years analysed, whereas for gentoo penguins this value was within the observed range of previous seasons. The observation of an extreme event of high wind intensity and low temperature at the end of October 2023, which caused an anomalous drop in wind chill temperature and also above average snow accumulation during November 2023, may explain the low breeding success observed in Adélie penguins. Furthermore, although we did not record colony arrival dates or egg-laying dates, field observations of the colonies at the end of November allow us to assume that during 2023/2024 the gentoo penguins began laying eggs several days later than was observed in previous seasons.

Moreover, for both species during 2023/2024 we observed a high rate of nest loss between the first count of nests with eggs and the count of nests with chicks ~15 days later. Thus, we infer that for both species there was a high rate of egg-hatching failure and/or a high rate of hatchling mortality in this season, probably related to the late winter extreme storms registered during October and the consequent delay in the early snowmelt, as well as the colder conditions overall throughout the whole trimester. Rain events were rather limited during December 2023, so nest flooding due to rain cannot be considered as a plausible explanation. However, this does not fully explain the contrasting reproductive success of Adélie and gentoo penguins during 2023/2024. Interestingly, in 2023/2024 the chick survival rate (considered in this study as the number of chicks that reached the crèche divided by the number of nests with chicks)

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was the highest recorded for gentoo penguins during the analysed period, whereas for Adélie penguins it was slightly lower compared to other seasons. We suggest that these differential responses reflect species phenological differences and high food availability during the chick-rearing stage in the 2023/2024 season, as inferred from the penguins' foraging behaviour and the chicks' weight.

Prey abundance and quality may have strong influences on breeding chronology and success (e.g. Ballard *et al.* 2010, Lescroël *et al.* 2010, Cimino *et al.* 2014, etc.). During the breeding season, *Pygoscelis* penguins are central-place foragers and hence depend on local food resources for the daily provisioning of chicks. Foraging trip characteristics have been proposed as good predictors of food availability in the vicinity of the colony (Carpenter-King *et al.* 2017, Salmerón *et al.* 2023, Machado-Gaye *et al.* 2024). Previous studies of foraging behaviour on Adélie and chinstrap penguins in the South Shetland Islands showed that shorter foraging trips in both duration and distance during the 2019/2020 breeding season reflected high krill abundance assessed by acoustic monitoring (Salmerón *et al.* 2023, Machado-Gaye *et al.* 2024). Thus, given that Adélie penguin foraging trips during the 2023/2024 breeding season were similar in duration and distance to trips made during 2019/2020, being the shortest trips in the 5 years of study, we infer that there was a high availability of krill in the area during the 2023/2024 season. Furthermore, the masses of fledglings during 2023/2024 were the highest recorded for Adélie penguins and the second highest recorded for gentoo penguins, which is consistent with conditions of high food availability during chick-rearing. Thus, low food availability appears to be an unlikely explanation for the low reproductive success of Adélie penguins on Ardley Island during the 2023/2024 breeding season, which is in agreement with previous observations by Machado-Gaye *et al.* (2025). However, it may have been an important factor in the reproductive success of gentoo penguins, as the observed high survival rate of chicks to crèche may actually be a consequence of high food availability. Gentoo penguin chicks require a greater amount of food compared to chicks of Adélie penguins and exhibit lower growth rates, typically fledging after an average of 72 days, whereas Adélie penguin chicks fledge after 52 days (Trivelpiece *et al.* 1987). Delayed laying (or even re-laying after failure) and a longer chick-rearing stage with high food availability might have provided gentoo penguins the opportunity to recover from an exceptionally harsh onset of the breeding season.

It is worth noting that our study has some limitations in the amount of population parameter data collected over the five seasons. Such is the case for the 2020/2021 season, during which an extreme weather event also occurred at the beginning of the breeding season, with high snow accumulation and precipitation during October and November. Furthermore, when considering the foraging trip characteristics of both species and the chicks' weight, it would also appear to have been a season of low food availability. However, given the logistical restrictions caused by COVID-19 during that season, we were unable to record the number of nests with eggs and therefore the breeding success or the rate of successfully hatched eggs.

In summary, our results suggest that the breeding success of Adélie and gentoo penguins nesting on Ardley Island is influenced by a combination of characteristics of their life history, weather conditions and food availability during the breeding season. These observations warn against the risks of drawing misleading conclusions derived from considerations of only some of these factors and highlight the need for integrated monitoring programmes that simultaneously record information on all of these dimensions. Current climate projections for the Antarctic Peninsula project a continued shift towards warmer conditions, along with an increase in precipitation, wind speed and the length of the snowmelt season (Siegert *et al.* 2019, Bozkurt *et al.* 2021). This could reduce food resources and affect weather conditions during the breeding season, directly influencing the reproductive success and population trends of *Pygoscelis* penguins. Furthermore, there are other key factors in interpreting population trends for these species, such as those operating during the non-breeding season. Overwinter conditions faced by juveniles and adults may affect their survival, with consequences for recruitment and the conditions under which potential breeders initiate the next breeding season, hence affecting the size of breeding populations (Hinke *et al.* 2007, 2012). Regarding this, it is also essential to consider how factors such as food availability during the breeding season determine the body condition with which juveniles and adults begin the wintering season. The high energetic costs faced by adults to meet the energetic demands of their offspring during seasons of low food availability may result in poorer adult body condition for the coming winter season (Machado-Gaye *et al.* 2025), while for fledglings the first weeks of independence represent a bottleneck in their survival that is also related to their body condition (i.e. body mass; Hinke *et al.* 2007).

Supplementary material. To view supplementary material for this article, please visit http://doi.org/10.1017/S0954102025100291.

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Competing interests. The authors declare none.

Author contributions. All authors conducted fieldwork and contributed ideas to the paper's development as well as edits to the manuscript. ALM-G, GM and AS analysed the data and led the writing of the manuscript.

Dedication. This article is dedicated to the memory of Andrés Barbosa, a friend who introduced us to the fascinating world of penguins and polar research.

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