IBIS
BOU international journal of avian science

Ibis (2026) doi: 10.1111/ibi.70030

UAV-based terrain metrics reveal species-specific nest-site preferences in *Pygoscelis* penguins

MAŁGORZATA KORCZAK-ABSHIRE,*[1] KATARZYNA EWA JAWORSKA,[2] PIOTR PABJANEK,[2]
MARLENA KYCKO[2] & ANNA ZMARZ[2]
[1] *Institute of Biochemistry and Biophysics, Polish Academy of Sciences, Pawińskiego 5a, 02-106, Warsaw, Poland*
[2] *Department of Geoinformatics, Cartography and Remote Sensing, Faculty of Geography and Regional Studies, University of Warsaw, Krakowskie Przedmieście 30, 00-927, Warsaw, Poland*

Ongoing climate change and glacial retreat are expanding ice-free areas in Antarctica, offering new potential breeding habitats for marine birds such as penguins. This study examines the relationship between terrain features and the nesting distribution of three species of *Pygoscelis* penguins in the Western Antarctic Peninsula, a region experiencing rapid climate change, fishing pressures, and shifts in penguin species abundance and distribution. Here, we used remote sensing and geospatial analysis to process digital terrain models and orthophotos obtained from fixed-wing unmanned aerial vehicle (UAV) beyond visual line of sight (BVLOS) surveys (94.82 km and 104.20 km flights at altitudes of 350 m above sea level) in the South Shetland Islands, allowing detailed analysis of a selected 35-ha subset of the larger surveyed dataset. Statistical analyses confirmed selectivity in nest location and breeding ground choice by Adélie *Pygoscelis adeliae*, Gentoo *Pygoscelis papua* and Chinstrap *Pygoscelis antarcticus* Penguins. Adélie Penguin nesting areas differed from their surroundings in more relief variables than the nest-sites of Gentoo and Chinstrap Penguins. For all three species, at least one variable clearly distinguished breeding sites from the adjacent landscape. Adélie Penguins nested in higher, more inland areas, while Chinstrap Penguins occupied lower, coastal sites with steeper slopes and greater topographic variability. Gentoo Penguins used sites with the lowest hydrological risk, Chinstrap Penguins occupied sites with moderate water-accumulation conditions and Adélie Penguins nested in areas with the highest potential water accumulation, reflecting distinct ecological strategies across species. Our findings highlight preferred breeding conditions for each species, such as areas with minimal snow and water accumulation and a tendency toward low slope and northern exposure. These insights into nesting site selection could inform conservation efforts. The UAV BVLOS-based method demonstrated high efficiency and minimal disturbance, suggesting its suitability for further applications in penguin habitat monitoring and research.

Keywords: Antarctic specially protected areas, breeding ecology, habitat heterogeneity, seabirds, South Shetland Islands.

Nest-site selection may be consistent throughout a species' range or may vary depending on habitat availability and regional constraints on nesting success (Pratte *et al.* 2016, Schmidt *et al.* 2021, Colombelli-Négrel & Iasiello 2023). This process is central to reproductive performance and population trends, and is of current interest, particularly for colonial birds inhabiting rapidly changing Antarctic regions. In these areas, glacial retreat is expanding ice-free land (e.g. Lee *et al.* 2017, Convey & Peck 2019), creating new potential breeding habitats for marine birds such as penguins. However, species are expected to differ in their site preferences and in microhabitat requirements (Trivelpiece & Volkman 1979, Trivelpiece

---

*Corresponding author.
Email: mka@ibb.waw.pl

et al. 1987, Moczydłowski 1989, Ainley 2002, Boersma 2008). Pygoscelid penguins are an important component of the Antarctic ecosystem. Although their global population has declined from an estimated 10.23 million (1990) to 7.64 million pairs (Woehler 1995, Lynch & Larue 2014, Herman *et al.* 2020, Strycker *et al.* 2020), they still account for over 90% of Antarctic bird biomass in the West Antarctic Peninsula (WAP) and the Scotia Sea (Dunn *et al.* 2016 and references therein). In the WAP region, the ranges of Adélie *Pygoscelis adeliae*, Chinstrap *Pygoscelis antarcticus* and Gentoo *Pygoscelis papua* Penguins overlap, yet their population trends diverge: Adélie and Chinstrap populations are declining, whereas Gentoo Penguins are increasing and expanding southward (e.g. Korczak-Abshire *et al.* 2013, 2019, Sierakowski *et al.* 2017, Herman *et al.* 2020, Strycker *et al.* 2020). The region is undergoing rapid climate change, shifts in prey availability and intensified commercial fishing, all of which may be influencing regional biodiversity and food web dynamics (Hinke *et al.* 2017, Watters *et al.* 2020). Although Pygoscelid penguins spend most of their lives at sea, they rely on snow-free land for breeding, chick rearing and moulting, making terrestrial habitat essential for reproductive success, offspring survival and, ultimately, population dynamics (Müller -Schwarze 1984, Quintana 2001, Ainley 2002, Patterson *et al.* 2003).

Nest-site selection is a hierarchical, multi-scale process influenced by both abiotic factors – such as elevation, slope and microclimate – and biotic pressures, including predation risk, social interactions, access to resources and competition (Martin 1998, Jones 2001). As a result, birds often face trade-offs when selecting nest-sites, balancing the benefits and risks associated with each potential location. For example, elevated or wind-exposed terrain can reduce flooding and snow accumulation but may increase visibility to predators due to the 'edge effect' – namely, increased predation risk at habitat boundaries (Massaro *et al.* 2001, Korne *et al.* 2020). Territoriality, phenology and the distribution of high-quality sites can further intensify intra- and interspecific competition (Kildaw 1999, Gjerdrum *et al.* 2005). In some cases, birds may also rely on social information, selecting sites near conspecifics even when environmental conditions are suboptimal (Betts *et al.* 2008).

During the austral summer, *Pygoscelis* species exhibit disparate breeding behaviours (e.g. Lishman 1985). Nevertheless, all species form breeding colonies on ice-free terrain, either in monospecific or mixed groups, and construct nests from pebbles (Volkman & Trivelpiece 1981). Some species are known to occupy territories or practice pairing close to the natal site (Ainley 2002). It can be reasonably assumed that the breeding territory with the best chances for reproductive success is likely to be the most favoured. In densely packed penguin colonies, microtopographic variation creates nesting sites that are locally optimal with respect to factors such as drainage, thermal exposure and accessibility, with the relative importance of these factors changing over time. All Pygoscelid penguins breed during the peak of the Antarctic summer (Borboroglu & Boersma 2013), sharing biparental incubation but differing in timing and shift patterns (Trivelpiece *et al.* 1987). Gentoo Penguins are semi-migratory and often remain at colonies year-round (Trivelpiece & Trivelpiece 1990, Korczak-Abshire *et al.* 2021) whereas Adélie and Chinstrap Penguins migrate long distances, arriving in early October and November, respectively (Hinke *et al.* 2015, 2019, Black 2016). Breeding success depends on nesting timing and accessibility, which are influenced by sea-ice cover and weather-driven land conditions.

The topography of *Pygoscelis* penguin rookeries was first described qualitatively (Jabłoński 1984a, 1984b, Quintana 2001, de Neve *et al.* 2006). Technological advances now enable high-resolution environmental analysis through structure-from-motion photogrammetry and Geographic Information System (GIS)-based terrain modelling, offering new tools for testing hypotheses about nest-site selection (Korne *et al.* 2020). Subsequent studies have applied remote sensing and digital mapping to identify Antarctic avifauna breeding areas and analyse terrain characteristics (Mustafa *et al.* 2017, Oosthuizen *et al.* 2020, Schmidt *et al.* 2021, Santa Cruz & Krüger 2023). Digital terrain models (DTMs) have also been used to investigate how terrain influences Adélie Penguin habitat selection, demography and reproductive success (Patterson 2001, Schmidt *et al.* 2021).

The nest-site preferences of *Pygoscelis* penguins from King George Island, South Shetlands, were first quantified and described by Volkman and Trivelpiece (1981), who reported intense competition linked to population increases driven by enhanced krill (Euphausiacea) availability in former whaling areas (Trivelpiece & Volkman 1979). In this study, we re-evaluated nest-sites at the same locations on King George Island (Volkman & Trivelpiece 1981, Jabłoński 1984b), and on the neighbouring Ardley Island using unmanned aerial vehicle (UAV) photogrammetry and geospatial analysis. In addition to the existing open-source data for Ardley Island (Mustafa & Pfeifer 2014), long-range, beyond visual line of sight (BVLOS) UAV flights were conducted to collect photogrammetric data for generating high-resolution digital terrain models and orthophotos of Admiralty Bay's west coast on King George Island (c.7 km^2; Zmarz *et al.* 2018, 2023). These datasets provide a high-resolution alternative to ground-based and satellite imagery, which are often limited in coverage and spatial resolution (McDowall & Lynch 2017, 2019, Schmidt *et al.* 2021). We investigated the spatial characteristics and potential preferences of *Pygoscelis* penguin nest-sites by testing two hypotheses: (1) terrain features differ significantly between nest-sites and non-nesting areas and (2) each *Pygoscelis* penguin species exhibits distinct nest-site preferences.

METHODS

Investigated penguin rookeries

We studied *Pygoscelis* penguin breeding colonies located in two Antarctic Specially Protected Areas (ASPAs) on King George Island (ASPA No. 128) and Ardley Island (ASPA No. 150) in the South Shetland Islands, Western Antarctic (Fig. 1). Analyses were conducted on three species: Adélie *P. adeliae*, Gentoo *P. papua* and Chinstrap *P. antarcticus* Penguins. Rookeries were studied at Point Thomas and Llano Point, where Adélie and Gentoo Penguins occupied separate areas. Single-species rookeries included Gentoo Penguins at Ardley Island and Chinstrap Penguins at Uchatka and Patelnia Point at Admiralty Bay's west coast. The colonies comprised birds of varying ages. Seven single-species sub-areas, each measuring 5 ha, were delineated (Fig. 1). One penguin species' breeding site was examined in each sub-area. The abundance and recent trends of the investigated populations are presented in the Supporting Information (Fig. S1). Terrestrial ice-free areas have changed over time, creating possible new nesting habitats. In ASPA 128, 6.1 km^2 of land became ice-free over 39 years (Pudełko *et al.* 2018).

Digital terrain model and orthophoto

The DTMs were derived from two sources. The first was the DTM of Ardley Island (ASPA 150) with a ground sampling distance (GSD) of 10 cm, originally downloaded on 3 April 2015 from http://www.think-jena.de/daten1-1_en.php (now available at https://zenodo.org/records/14614877). The open source data were provided by the Turin Institute for Sustainable Development and Climate Protection ThINK (Mustafa & Pfeifer 2014). The second dataset was the ASPA 128 King George Island DTM, based on imagery derived from BVLOS UAV flights in November 2014 (Zmarz *et al.* 2015, 2023), and SCAR data as part of the Antarctic Digital Database. Photogrammetric flights over ASPA 128 were conducted on 11 November and 6 December 2014 (IBB PAS Permit No. 6/2014, ATCM38_ip077_e), when individuals of each species were incubating eggs in visible and separate breeding groups. The UAV flights were performed autonomously using an autopilot linked to a telemetry module. They were carried out by a team of three, all holding BVLOS licences issued by national authorities. ASPA 128 was photographed using a fixed-wing PW-ZOOM UAV equipped with a Canon 700D digital SLR camera and a Canon 35-mm f/2.0 lens. Both flights were conducted at an altitude of 350 m above sea level, with total distances of 94.82 km (11 November) and 104.20 km (6 December). The UAV flights were designed to cover the west coast of Admiralty Bay (ASPA 128), with take-off and landing points located near the Arctowski Research Station. The images were captured with a 70% forward overlap and a 60% side overlap. All collected images had a GSD of less than 5 cm (Zmarz *et al.* 2015, Rodzewicz *et al.* 2017). The ASPA 128 terrain model and orthophoto were generated using Agisoft PhotoScan (Agisoft 2015). The WGS-84 Antarctic Polar Stereographic System (EPSG:3031) was used to model King George Island for consistency with Antarctic Digital Database data.

Terrain features

Based on existing literature (Volkman & Trivelpiece 1981, Moczydłowski 1989, Trivelpiece &

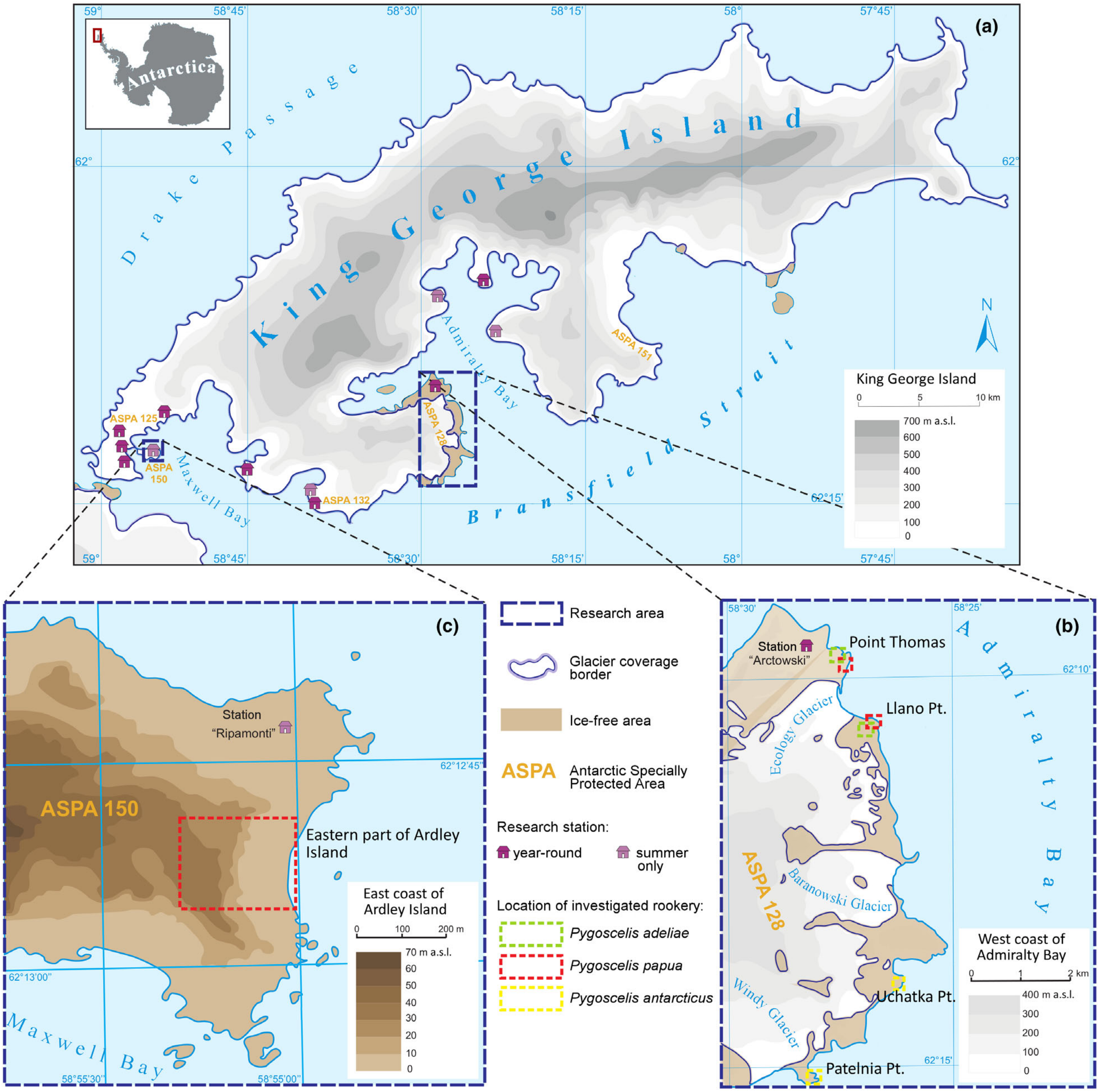

Figure 1. The study areas were located at the southwest coast of King George Island (South Shetland Islands, Antarctica) (a). The analysis included two rookeries at Point Thomas and Llano Point, both hosting Adélie and Gentoo Penguins in spatially separated nesting areas, and two single-species Chinstrap Penguin rookeries at Uchatka and Patelnia Point in the Antarctic Specially Protected Area (ASPA) No. 128 on the west coast of Admiralty Bay (b) and a single-species Gentoo Penguin rookery at the Antarctic Specially Protected Area No. 150 on the western part of nearby Ardley Island (c). Adapted from figures 2, 3 and 5 in Jaworska (2016).

Fraser 1996, Quintana & Cirelli 2000, Boersma 2008), the following types of terrain characteristics were selected for analysis: elevation above sea level (m a.s.l.); distance from shore (m); slope (°); exposure (the compass direction that a terrain surface faces); flow accumulation (hydrological conditions); solar radiation intensity; as well as terrain roughness (microrelief). Monthly solar radiation (kWh/m^2/month) was calculated for the period from 1 to 30 November, when the breeding season had already started for all three species. Terrain roughness was an available geomorphological parameter treated as an expression of small-scale topographic variability (Grohmann *et al.* 2011).

Geoinformatics analyses

A series of geospatial analyses was conducted using a DTM with a 1-m GSD and orthophotos with 10- to 20-cm GSD. The orthophoto was used to delineate seven research sub-areas manually according to the spatial distribution of the breeding colonies. Each was rectangular (with a strong resemblance to a square) and had an area of 5 ha (see Fig. 1). These research sub-areas were restricted to land only. However, narrow patches of sea were sometimes included to keep the nesting groups in the centre of the photo. On the orthophotos, breeding group boundaries (pink polygons in Fig. 2) were manually delineated in ArcMap using the *Create Features* tool, based on nest clustering, inter-nest distances and visible landscape features. Selected nests within these groups (marked as 'points within breeding groups' in Fig. 2) were analysed. The number of these points was proportional to the size of the breeding group (Table 1). Terrain features characteristic of non-breeding grounds were identified at 'random points' across seven delimited research sub-areas. The random point distribution within each research sub-area had a density of 5/ha (using the ArcMap software tool *Random Points*). Each point (random and within breeding groups) was assigned corresponding values of the study variables. This assignment was performed using ArcMap tools: *Slope*, *Aspect*, *Flow Accumulation* and *Area Solar Radiation*, with the last calculating potential solar radiation under clear-sky conditions, not accounting for clouds or indirect reflections, providing a standardized metric for site comparison. Additionally, the mean and standard deviation of the feature 'nest distance from shore' were calculated for the three species using the ArcMap tool *Near* for distance from shore and *Extract Values to Points* for elevation.

An additional set of points (marked as 'points within 5-m buffer' in Fig. 2) was used to examine terrain roughness. This analysis aimed to determine whether there were any discernible disparities in relative height within the immediate vicinity of the nest groups and to assess whether birds were more likely to establish breeding sites on small elevations, such as hills or ridges, within the local topography. Visual analysis of the DTM showed the most significant changes in slope within 5 m of nest group boundaries. A 5-m buffer zone was created around each breeding group, with the number of selected 'points within 5-m buffer' distributed equally among the corresponding group (Fig. 2). Terrain roughness was therefore compared across three categories: the slope at the breeding groups (representing nests), within the 5-m buffer zone and at random points. Most of the results are presented as boxplots generated using the *ggplot2* package (Wickham 2016) in the R statistical environment (version 4.4.1; R Core Team 2024). Exposures are presented using radar diagrams to illustrate the contribution of each direction to the total exposure at the surveyed points. Flow accumulation was expressed as the number of 1-m cells in the regular grid into which the terrain had been divided. It represents the number of cells through which water must flow to reach the point under study from the watershed boundary. The results are divided into four classes (0, 1–5, 6–100 and ≥101) and expressed as percentages. The class ranges were selected manually based on the distribution of values in the histogram. Cells with a flow accumulation value of 0 correspond to local topographic highs and were used to identify ridges. In contrast, cells with high flow accumulation represent areas of concentrated flow and help identify stream channels (e.g. Jenson & Domingue 1988).

To test the first hypothesis – that terrain features differ significantly between nest-sites and non-nesting areas – a comparative analysis of terrain variables was conducted between nest locations (points within breeding groups) and random points drawn from two groups: (1) random points within sub-areas adjacent to the nesting site of each species: two sub-areas for Adélie (50 points), three sub-areas for Gentoo (75 points) and two sub-areas for Chinstrap Penguins (50 points), these representing the surrounding areas occupied separately by each species; and (2) random points within the entire study area: a total of 175 points from the seven sub-areas were analysed, serving as a reference to the general environment surrounding the nest-sites of all three species combined.

The Mann–Whitney *U*-test was used to determine statistically significant differences between groups. The presented figures indicate whether the difference between the samples was statistically significant at the $P < 0.005$ level. The text

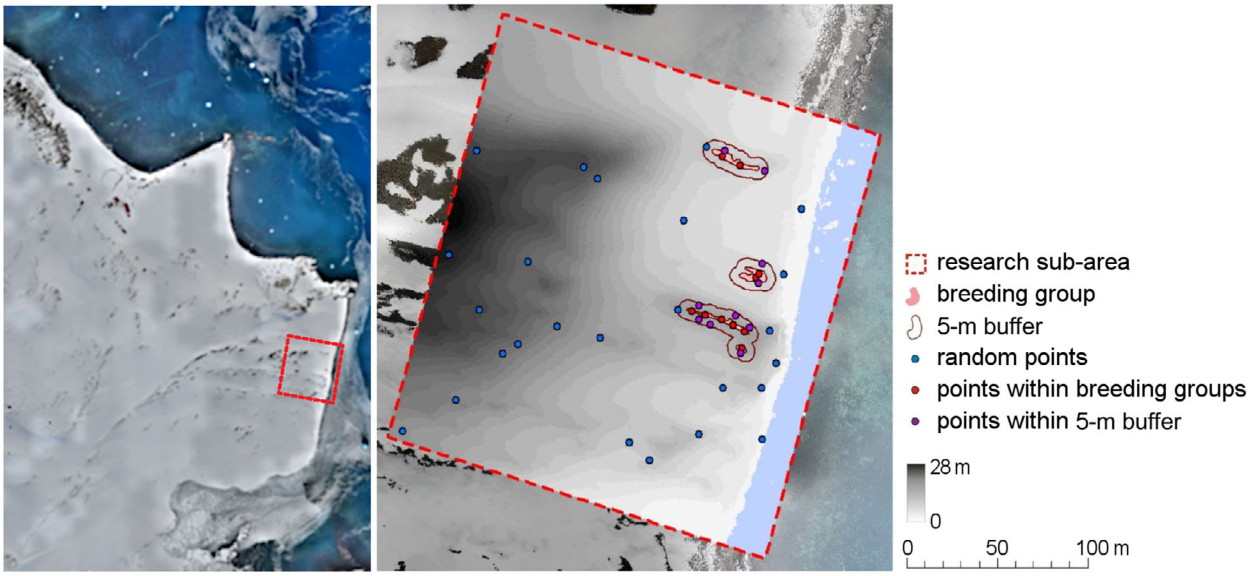

Figure 2. Distribution of measuring random points, points within breeding groups and within 5-m buffers in the research sub-area of Gentoo Penguin breeding groups at Point Thomas. A section of the Digital Terrain Model is shown against an orthophoto background.

Table 1. Data on *Pygoscelis* for seven research sub-areas, number and area size of breeding groups, and selected measurement points (both random and within breeding groups representing nests). ARDL, Ardley Island; LLAN, Llano Point; PAPT, Patelnia Point; PTHO, Point Thomas; UCHA, Uchatka.

Species	Colony name	Research sub-area size (ha)	Number of breeding groups within research sub-area	Size of the area occupied by breeding groups (m^2)	Number of measurement points	
					Nest number	Random points
Adélie	PTHO	5	10	3600	25	25
	LLAN	5	4	1800	20	25
Gentoo	LLAN	5	24	6300	25	25
	PTHO	5	4	250	10	25
	ARDL	5	41	1300	25	25
Chinstrap	UCHA	5	6	700	25	25
	PAPT	5	3	300	15	25
Total	-	35	91	14 250	145	175

provides detailed test results, including median values (M_g, median for nests; M_p, median for random points within sub-areas adjacent to the nesting site of each species; M_{tp}, median for random points within the entire study area; M_b, median for 5-m buffers) and the *U*-test value. While $P < 0.05$ is typical for naturalistic studies, this study used a more rigorous threshold of $P < 0.005$. To assess penguin preference for a terrain feature, a coefficient of variation was calculated. The coefficient of variation was calculated by dividing the standard deviation by the sample mean and multiplying the result by 100 to obtain a percentage figure (Everitt 2002). A lower coefficient indicates a stronger preference for a particular terrain feature. To verify the results, coefficients of variation were also calculated for the random points. These analyses allowed for the assessment of whether a high concentration of scores resulted from low variability of a site feature across the study area. To test the second hypothesis – that each *Pygoscelis* species exhibits distinct nest-site preferences – nest-site characteristics among the three species were compared. This was accomplished using the Kruskal–Wallis test, a non-parametric method by which statistically significant differences in variable distributions among the three species were evaluated. Although this test can detect overall interspecies differences, it does not indicate which specific pairs differ. Therefore, Dunn's test with post-hoc pairwise comparisons was conducted. The results are presented in the same way, in the form of boxplots (*ggplot2*, R version 4.4.1). The statistical analyses were conducted using *Real Statistics* (Zaiontz 2016), an open-source software package that extends Excel statistical functions.

RESULTS

Adélie Penguins

In the selected breeding colonies, Adélie Penguins nested in open areas, with an average distance from the shore of 167 m (standard deviation (sd) = ±57 m; Fig. 3a). The Mann–Whitney *U*-test showed that nests were located at higher elevations (M_g = 44.9 m a.s.l) than random points in adjacent areas (M_p = 34.9 m a.s.l., U = 1688, $P < 0.005$; Fig. 3d), and also higher than random points across the entire study area (M_{tp} = 24.6 m a.s.l., U = 7063, $P < 0.005$). Adélie Penguin breeding grounds had a gentle slope of about 6°, which was significantly lower than the slope of adjacent areas (M_p = 10°, P = 0.003) and the entire study area (M_{tp} = 9°, $P < 0.001$; Fig. 3g). Within 5-m buffers around nests, slope was significantly higher than at nest locations themselves (M_b = 8.3°, U = 1352, P = 0.006). Overall, these results indicate that Adélie Penguins

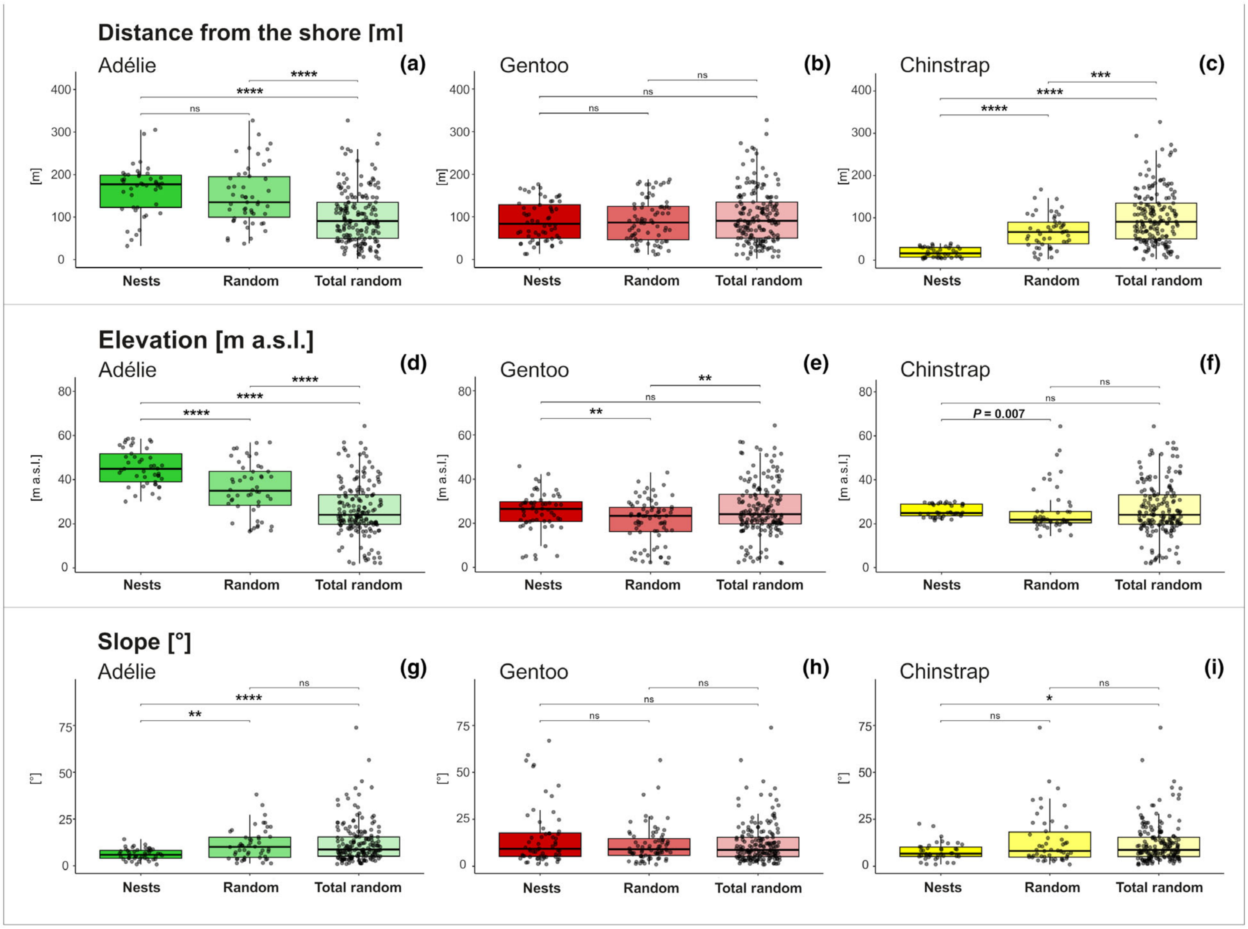

Figure 3. The median (horizontal line), minimum and maximum values (whiskers) for elevation (m a.s.l.), distance from the shore (m) and slope (°) at Adélie (a, d, g), Gentoo (b, e, h) and Chinstrap (c, f, i) Penguin nest-sites (Nests), random points in adjacent areas (Random, specific to each species) and random points across the entire study area (Total random). Horizontal brackets with asterisks indicate statistically significant differences based on the Mann–Whitney *U*-test (ns = not significant, $P \geq 0.05$; *$P < 0.05$; **$P < 0.01$; ***$P < 0.005$; ****$P < 0.001$).

nest on relatively gentle terrain compared with their surroundings. There were no major terrain obstacles in the breeding area; consequently, solar radiation was uniformly high and exhibited very low variation (2%). The Mann–Whitney *U*-test detected no significant difference in solar radiation between Adélie Penguin nest-sites (M_g = 119.1 kWh/m^2/month) and adjacent areas (M_p = 120.4 kWh/m^2/month, U = 932, P = 0.453), nor between nest-sites and the entire study area (M_{tp} = 117.4 kWh/m^2/month, U = 4563, P = 0.300). Most nests (55.6%) were situated on well-lit northwesterly slopes (Fig. 4), which received strong sunlight in the southern hemisphere. Random points in adjacent areas were also predominantly northerly (64% for north, northeast and northwest); however, shaded areas (e.g. terrain depressions or sites with unfavourable exposure) reduced mean solar radiation. Adélie Penguin nests were located in areas with divergent flow accumulation patterns. Across the study area, 40% of nests had zero flow accumulation, but this varied markedly between sub-areas: in the Llano Point area, 65% of nesting points had no accumulation, whereas in Point Thomas only 20% had none. However, nest-sites had much lower flow accumulation (M_g = 4, expressed as the number of 1-m^2 grid cells contributing flow) than random points in the adjacent area (M_p = 18 grid cells; U = 711, $P < 0.01$) and the entire study area (M_{tp} = 14 grid cells; U = 2675, $P < 0.005$). The two sets of random points did not differ significantly (U = 4645, P = 0.506).

Gentoo Penguins

The average distance between Gentoo Penguin nests and the shoreline was 90 m (sd = ±46 m; Fig. 3b). No significant differences were found between nest-sites and either group of random points (all $P > 0.999$). Elevation at nest-sites showed considerable variation (mean 25.3 m a.s.l., sd = ±9.0 m), with nests located significantly higher than adjacent random points (M_g = 26.5 m a.s.l., M_p = 23.4 m a.s.l., $P < 0.05$; Fig. 3e). However, no elevation difference was detected between nests and random points distributed across the entire area (M_{tp} = 24.1 m a.s.l., $P > 0.999$). No statistically significant differences were observed between nests and random points for terrain slope (M_g = 9.3°, M_p = 9.0°, M_{tp} = 8.7°, $P > 0.999$; Fig. 3h). No evidence was found that Gentoo Penguins select nest-sites based on slope, as comparisons between nest-sites, 5-m buffer zones and adjacent random points showed no significant differences. Nonetheless, the slope within buffer zones was steeper (M_b = 14.9) than that of the surrounding landscape. No statistically significant differences were observed between nests and random points for solar radiation intensity (M_g = 116.8 kWh/m^2/month, M_p = 117.2 kWh/m^2/month, M_{tp} = 117.4 kWh/

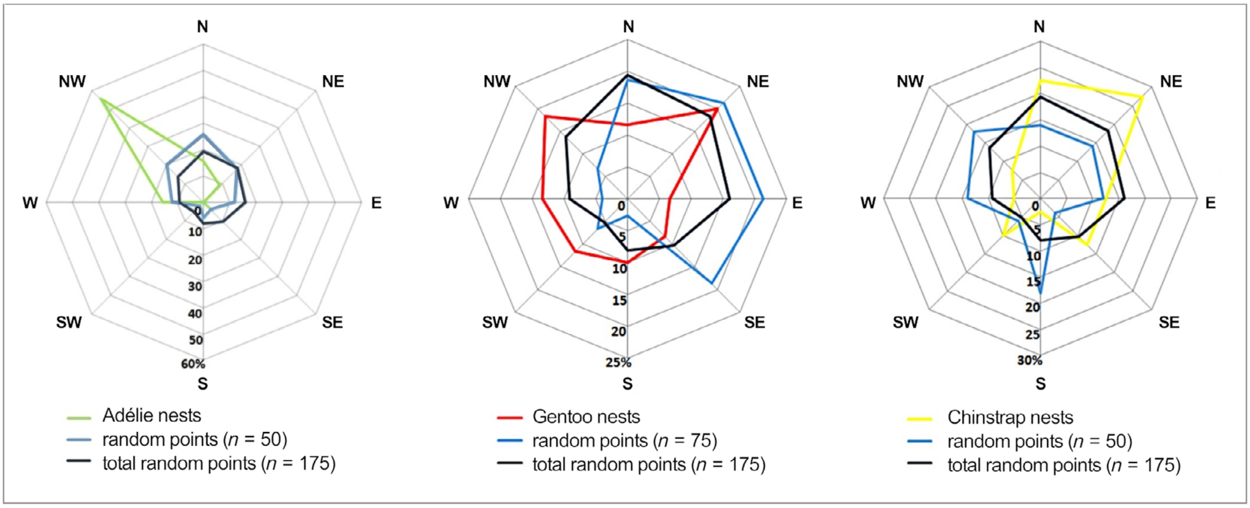

Figure 4. Exposure of Adélie, Gentoo and Chinstrap Penguin nesting areas, random points in adjacent areas (random points) and the entire study area (total random points).

m^2/month, $P > 0.999$). Nest-sites occurred on slopes with diverse exposure angles, with approximately half facing near-northern directions – specifically northeast (20%), northwest (18%) and north (12%). Random points in the surrounding terrain with north, northeast or northwest exposures comprised slightly less than 47% of the sample. However, clear differences emerged in east–west exposure patterns. Slopes with northwest, west and southwest aspects accounted for over 43% of nest-sites but only 17% of random points within sub-areas adjacent to the nest-site. By contrast, slopes facing northeast, east or southeast comprised 35% of nests, compared with approximately 63% for random points within sub-areas (Fig. 4). Gentoo Penguins showed a strong preference for nesting in areas with low flow accumulation. The majority of nests (79%) were located in areas with zero flow accumulation, whereas only 31% of random points shared this feature. Across nesting areas, flow accumulation values were relatively evenly distributed across the lower three classes: 0 (79%), 1–5 (13%) and 6–100 (8%). No points fell into the highest class (≥101), which typically corresponds to stream channels.

Chinstrap Penguins

Chinstrap Penguin nests were, on average, 18.5 m from the shoreline (sd ±11.9 m) and significantly closer to the shore ($M_g = 16.3$ m) than adjacent random points ($M_p = 66.6$ m; $U = 222$, $P < 0.005$), and random points across the entire study area ($M_{tp} = 90.7$ m; $U = 395$, $P < 0.005$, Fig. 3c). Chinstrap Penguin nests occurred within a narrow elevational range (mean 25.83 m a.s.l., sd = ±2.80 m). Nests were significantly higher ($M_g = 24.87$ m a.s.l.) than random points in the adjacent area ($M_p = 21.80$ m a.s.l., $U = 1378$, $P = 0.007$), which showed much greater elevational variability (mean 25.92 m, sd = ±10.40 m). No significant elevational differences were found between nest-sites and random points from the entire study area ($M_{tp} = 24.07$ m a.s.l., $U = 3809$, $P > 0.999$), nor between adjacent area and entire study area random points ($U = 4032$, $P > 0.999$; Fig. 3f). The median slope within Chinstrap Penguin breeding groups was 6.7°. Adjacent areas were steeper ($M_p = 8.2°$), but the Mann–Whitney *U*-test showed no significant difference between nest-sites and adjacent area random points ($U = 838$, $P > 0.5$). Similarly, there was no significant difference between nest-sites and random points from the entire study area ($M_{tp} = 8.7°$, $U = 2764$, $P > 0.1$). Within the 5-m buffers surrounding the nesting groups, the median slope was 14°. A significant difference was found between the 5-m buffer zones and the nest-sites ($U = 1208$, $P < 0.005$).

Solar radiation at the nesting sites ($M_g = 117.5$ kWh/m^2/month) did not significantly differ from random points around the Chinstrap Penguin colonies ($M_p = 115.62$ kWh/m^2/month, $U = 1135.5$, $P > 0.819$) or the entire study area ($M_p = 117.4$ kWh/m^2/month, $U = 3376.5$, $P > 0.999$). Most nests were on northeastern (27.5%) and northern (22.5%) slopes, with only 2.5% on southern slopes. The dominance of northeastern exposure was not solely the result of area availability, as random points showed different results (Fig. 4). Chinstrap Penguin nests were located in areas with significantly lower flow accumulation values compared with fully random points across the study area ($M_g = 5$ grid cells, $M_{tp} = 14$ grid cells, $U = 2475$, $P = 0.012$). No significant differences were found between nests and adjacent area random points ($P = 0.500$), nor between the two groups of random points ($P = 0.624$). Over half of the nests (55%) were in areas with zero flow accumulation, compared with 42% for adjacent area random points.

Comparison between *Pygoscelis* species

The results of the Kruskal–Wallis test indicated significant interspecific differences for elevation ($H = 84.72$, df = 2, $P < 0.001$), distance from the shore ($H = 100.32$, df = 2, $P < 0.001$) and slope measured within nests ($H = 13.5$, df = 2, $P = 0.001$) and 5-m buffers around the breeding groups ($H = 12.43$, df = 2, $P = 0.001$), whereas exposure, flow accumulation and solar radiation intensity showed no significant differences. Elevation above sea level was highest for Adélie Penguins, intermediate for Gentoo Penguins and lowest for Chinstrap Penguins (Fig. 5). Dunn's post-hoc test with Bonferroni correction revealed that Adélie Penguins nested significantly higher than both Chinstrap and Gentoo Penguins ($P < 0.0001$), with no significant difference between the latter two ($P > 0.999$). Distance from

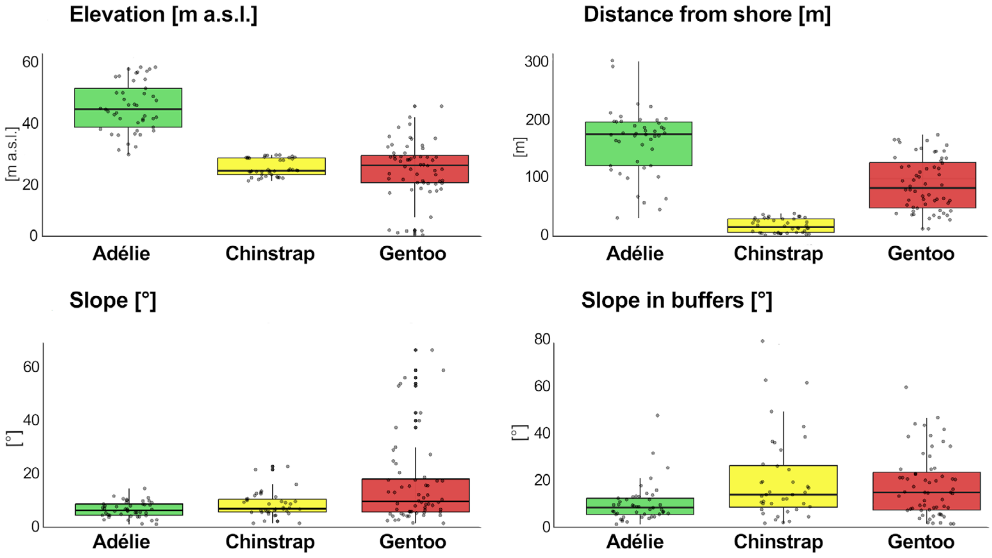

Figure 5. Elevation (m a.s.l.), distance from the shore (m), slope within nest areas (°) and slope within 5-m buffers (°) differed significantly among the three *Pygoscelis* species (Kruskal–Wallis tests, $P < 0.005$ for all variables). Each boxplot shows the variable's distribution: the thick line marks the median, the box the interquartile range and the whiskers the range of non-outlying values. Pairwise differences between species were evaluated using Dunn's post-hoc tests with Bonferroni correction.

shore followed the same order, with Adélie nests furthest inland, Gentoo at intermediate distances and Chinstrap closest to the shore (Fig. 5). Pairwise comparisons confirmed significant differences among all three species (Adélie versus Chinstrap: $Z = 9.99$, $P < 0.001$; Adélie versus Gentoo: $Z = 4.63$, $P < 0.001$; Chinstrap versus Gentoo: $Z = 6.17$, $P < 0.001$). Terrain slope at nest-sites varied significantly among penguin species (Kruskal–Wallis: $H = 13.50$, df = 2, $P = 0.001$). Dunn's test indicated that Adélie Penguins nested on significantly gentler slopes than Gentoo Penguins ($P < 0.001$), but no significant differences were found between Adélie and Chinstrap ($P = 0.391$) or between Chinstrap and Gentoo ($P = 0.167$) Penguins. Gentoo Penguins occupied steeper nest-sites, whereas Chinstrap Penguins occupied intermediate slopes. Slope in the 5-m buffers around nests also differed significantly among species, but here, Adélie Penguins showed significantly different preferences from both Chinstrap ($P = 0.0059$) and Gentoo ($P = 0.0069$) Penguins, which did not differ from each other ($P > 0.999$). This indicates that Adélie Penguins select breeding environments with distinct surrounding terrain, while Chinstrap and Gentoo Penguins share similar slope conditions around their nests. Solar radiation at nest-sites was highest for Adélie Penguins, slightly lower for Chinstrap Penguins and lowest for Gentoo Penguins. It was on the borderline of statistical significance ($H = 5.99$, df = 2, $P = 0.050$), but post-hoc Dunn's tests revealed that only the difference between Adélie and Gentoo Penguins was statistically significant ($P = 0.044$). The Kruskal–Wallis test showed that exposure ($H = 2.90$, df = 2, $P = 0.235$) and flow accumulation ($H = 0.10$, df = 2, $P = 0.95$) did not differ significantly among species. Although statistical differences in exposure were not detected, we observed a predominance of north-facing aspects, with nests oriented toward the north, northeast and northwest accounting for over 61% of all nests surveyed (Fig. 6). This pattern probably reflects the prevailing topography of the surveyed breeding areas rather than species-specific preferences, and therefore comparisons across species should be interpreted with caution. South-facing aspects were the least common, representing less than 5% of all nests.

Regarding hydrological conditions, only 40% of the Adélie nests were located in areas with zero flow accumulation, while 9% were in zones classified as having the highest flow accumulation risk (Table 2). Chinstrap Penguins showed a more favourable distribution, with 55% in zero-risk areas and only 2.5% in high-risk zones. Gentoo Penguins exhibited the most optimal conditions, with 79%

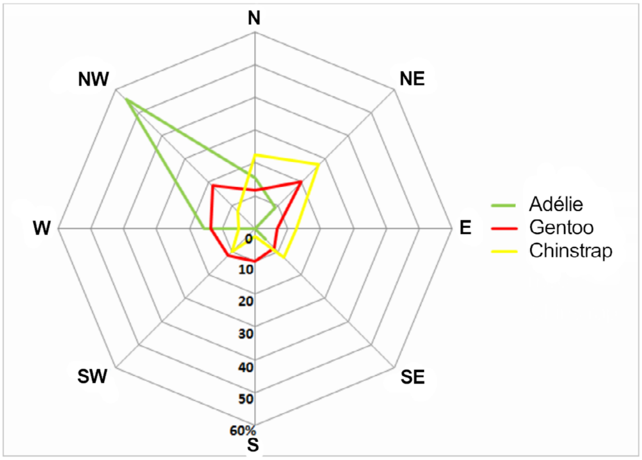

Figure 6. Exposure of each *Pygoscelis* penguin species' nesting area.

Table 2. Flow accumulation index values at the nesting areas of three *Pygoscelis* species.

Classified	Adélie (%; n = 45)	Gentoo (%; n = 60)	Chinstrap (%; n = 40)
0	40	79	55
1–5	26.5	13	37.5
6–100	24.5	8	5
≥101	9	0	2.5

of nests situated in areas without flow accumulation and none in the highest risk class.

DISCUSSION

Statistical analyses confirmed selectivity in nest location and specific preferences for the nesting area of each of the three *Pygoscelis* penguin species studied. This segregation in nest-site use between species allows relatively small ice-free areas of Antarctica to be fully occupied. Although species differences in nest-site selection may reflect intrinsic preferences, interspecific competition – where larger or earlier-nesting species potentially limit options for smaller or later-nesting ones – could also play a role. Adélie Penguin nesting areas exhibited a greater number of relief variables that significantly differed from the surrounding landscape compared with Gentoo Penguin sites, which displayed fewer distinct differences. Moreover, for each of the three species, at least one of the examined variables clearly differentiated the breeding sites from their surroundings. Adélie Penguins preferred nesting areas that were both higher in elevation and located farther from the shore, whereas Chinstrap Penguins selected sites that were lower and closer to the sea, with the steepest slopes and greatest topographic variability. Interestingly, Chinstrap nests were closer to the shore yet situated at higher elevations compared with random points in the surrounding area. Because a steadily rising slope from the shoreline would typically result in lower elevations near the coast, this pattern suggests that Chinstrap colonies occur on locally elevated landforms – such as raised marine terraces or topographic prominences near the shoreline. This topographic peculiarity indicates that Chinstrap Penguins may select shore-proximal sites that offer relief, potentially reducing flood risk. Differences in phenology may play a key role; Adélie and Gentoo Penguins in the WAP arrive about 2 weeks before Chinstrap Penguins (Black 2016), which influences the availability and suitability of nesting habitats. The earlier arrival of Adélie Penguins probably allows them to secure optimal high-elevation sites with more convenient conditions (i.e. less erosion, fewer landslides and less seasonal flooding), whereas the later arrival of Chinstrap Penguins may force them to use areas characterized by steeper slopes and greater topographic variability. Although traversing long distances and climbing steep slopes is energetically costly, these behaviours may help Adélie Penguins reach nesting sites with reduced snow cover, increasing their ability to start laying eggs on snow-free ground early in the season and lowering the risk of hazards associated with snowmelt. This suggests that they invest extra energy to access areas with minimal snow accumulation. This aligns with recent findings on the preference of Adélie Penguins for elevated nesting grounds in site selection (Gallagher *et al.* 2025). Our results are also consistent with earlier reports of Adélie Penguins' tendency to select nest areas with gentler slopes (Trivelpiece & Volkman 1979, Moczydłowski 1989, Chesalin *et al.* 2009). Adélie Penguins, highly colonial, nest where ice and snow are minimal and the ground is at least partially exposed (Trivelpiece & Volkman 1979, Jabłoński 1984b, Ainley 2002, Boersma 2008). The South Shetlands archipelago is one of the northernmost breeding sites for Adélie Penguins (Trivelpiece & Fraser 1996, Lynch & Larue 2014). This species is well-adapted to colder, drier regions, primarily breeding on the Antarctic continent. In these habitats, their tendency to breed in large groups facilitates snow melt – snow that melts faster because of a reduction in albedo – further aided by sodium chloride excretion, which lowers the melting point (Moczydłowski 1989). Large breeding sites are required, but on King George Island low-lying beaches are unsuitable because of water and snow accumulation at the beginning of the season. The most suitable areas are at higher elevations. Elevation was the most important terrain feature influencing nest-site selection across species. This agrees with previous findings that most Adélie Penguins nest at higher elevations (20–45 m, up to 80 m; Volkman & Trivelpiece 1981, Myrcha *et al.* 1987), whereas Chinstrap Penguin colonies are generally low-lying (0–30 m; Jabłoński 1984b, Macdonald *et al.* 2002). Our results follow this pattern: Adélie Penguins nested highest (median 44.9 m a.s.l.; interquartile range (IQR) 12.8 m), followed by Gentoo Penguins (26.5 m a.s.l.; IQR 8.91 m) and Chinstrap Penguins (24.9 m a.s.l.; IQR 5.42 m), reflecting the elevational gradients of King George Island. The narrow IQR for Chinstrap Penguin nests reflects the small, spatially constrained colonies studied, whereas larger colonies typically occupy a broader elevational range.

Despite clear habitat preferences, no site guarantees breeding success due to environmental variability and other ecological constraints. Not all nests will have equally favourable locations, and the selection of a suitable nesting site is also influenced by seasonal variations in conditions, and the age and breeding experience of the birds (Ainley 2002, de Neve *et al.* 2006, Cimino *et al.* 2019). Nevertheless, the analyses carried out identified preferred breeding conditions for each of the three species studied, including (1) low flow and water and/or snow accumulation potential and (2) a tendency toward low slope and northern exposure in contrast to the other two species. In the southern hemisphere, north-facing areas receive more sunlight, accelerating snowmelt and water evaporation. Studies have identified north-facing slopes as the primary locations for Adélie Penguin colonies (Jabłoński 1984a, Moczydłowski 1989, Aguirre 1995, Trivelpiece & Fraser 1996, Naveen & Lynch 2011). Patterson (2001) reported that colonies on Torgersen Island's north-facing slopes declined far less than those on south-facing slopes, highlighting northwest-facing slopes as the optimal nesting sites. Unfortunately, the studied population of Adélie Penguins on King George Island is declining dramatically (Fig. S1). The slope impacts nest stability, with water flow and stagnation posing significant risks to nestlings (Moczydłowski 1989, Boersma 2008). Our analysis suggests that water may pose the greatest threat to Adélie Penguin breeding grounds, particularly at the Point Thomas site, where only 20% of nests were located in zero-flow areas. Moreover, Adélie Penguins generally occupied zones with relatively unfavourable water accumulation conditions (see Table 2). Moczydłowski (1989) predicted that declining populations and expanding suitable terrain would drive colony shifts away from unfavourable sites, but we observed that many high-accumulation areas, historically linked to poor nesting success and elevated chick mortality, were still occupied for the last 20 years. Adélie Penguins exhibit strong natal philopatry, returning annually to the same colonies and even competing with their parents for nesting space (Ainley 2002). They also avoid new nesting sites – even when availability increases – because their colonial behaviour and site fidelity reduce exposure to unfamiliar-area predation (McDowall & Lynch 2019). This neighbour-preference strategy typically protects against skua predation (Schmidt *et al.* 2021) and probably reflects nest-site inertia and the benefits of conspecific clustering (McDowall & Lynch 2019). However, this behaviour may now constitute an ecological trap: Adélie Penguins evolved in cold, arid East Antarctica – where rain and surface runoff were once negligible (Ropert-Coudert *et al.* 2015) – and cue into traditionally 'dry' terrain, which no longer guarantees low water stress under a warming climate. In contrast, Gentoo Penguins – a more sub-Antarctic species accustomed to wetter conditions – show the strongest avoidance of flow accumulation zones (79% of nests in zero-flow areas). As precipitation and meltwater events become more frequent, Adélie Penguins' reliance on outdated environmental cues could trap them in increasingly unsuitable habitats, reducing reproductive success despite the continued appeal of familiar sites. Framing our results within an ecological-trap framework highlights the urgent need to monitor changing hydrological cues and reassess the assumed stability of long-used nesting areas.

In contrast to the other two species, Gentoo Penguins showed greater flexibility in their nest-site preferences. Their nesting locations were not significantly different from randomly selected points in most cases, except for elevation and flow accumulation, with Gentoo Penguins preferring slightly drier areas. The average slope value was 4.8° and was similar to that observed by other researchers (Volkman & Trivelpiece 1981, Quintana 2001). However, the slope within the 5-m buffer around breeding groups was higher than that observed on the breeding sites and surrounding areas. This was because Gentoo Penguin nests were typically located on flat or gently sloping terrain, surrounded by steeper slopes. They usually choose outcrops, terraces and moraines, which offer well-drained areas, further reducing the risk of water damage to their nests (Jabłoński 1984b, Moczydłowski 1989, Aguirre 1995, Quintana 2001, Korczak-Abshire *et al.* 2013). Although Gentoo Penguins tended to occupy sites in higher places earlier in the breeding season (Jabłoński 1984b, Chesalin *et al.* 2009), they are more opportunistic and adaptable in their choice of nesting sites (Volkman & Trivelpiece 1981, Quintana 2001). This was evidenced by our own observations using a network of photo traps over a 10-year period (unpubl. data). According to Quintana (2001), the most important feature was the availability of pebbles, which are needed for nest-building. Gentoo Penguin nests showed weaker north orientation than Adélie Penguin nests but were on flat or gentle slopes, often near hilltops, where exposure may be less crucial. The global population of Gentoo Penguins is stable or growing (Baylis *et al.* 2013, Herman *et al.* 2020), and this is also the case in the studied areas (Fig. S1). Gentoo Penguins' ability to select seasonally optimal breeding sites may contribute to this. Gentoo Penguins from the WAP region are probably less tied to traditional breeding sites than their sub-Antarctic counterparts (Williams & Rodwell 1992), reflecting their adaptability to environmental changes. Rapid population growth and the establishment of new colonies, especially in the WAP and farther south, have been documented (e.g. Herman *et al.* 2020, Korczak-Abshire *et al.* 2021).

Unlike the more adaptable Gentoo Penguins, Chinstrap Penguins presented a more complex pattern of nest-site selection, making their habitat preferences harder to define. This may be because the sample was less representative than for the other species. King George Island has numerous Chinstrap Penguin colonies, but relatively few of them are in the area under investigation. Most colonies are on the island's north side (Jabłoński 1984a, Strycker *et al.* 2020). The study covered only a fraction of the population, particularly Patelnia Point and Uchatka, which we have observed to decline by about 91% over 40 years (Fig. S1). Myrcha *et al.* (1985) noted that Chinstrap Penguin colonies were near the coast and Volkman and Trivelpiece (1981) found that the average distance of the Point Thomas Chinstrap Penguin colony (which no longer exists) from the nearest beach was 93 m. It should be noted that our study measured the distance of the nests from the coast, not landing beaches. The values do not necessarily correspond to the penguins' actual walking distance to the ocean. This is particularly important in the case of Chinstrap Penguins, whose colonies are often located in hard-to-reach places. Earlier reports (Volkman & Trivelpiece 1981, Müller-Schwarze 1984, Myrcha *et al.* 1985) describe Chinstrap Penguins nesting on steep slopes. Our results for Chinstrap Penguin nests showed a wide range of slope values (see Fig. 5). According to de Neve *et al.* (2006), breeding success of Chinstrap Penguins decreased with steeper slopes. The nesting sites surveyed were bounded on one or more sides by steep cliffs and on the other by relatively flat terrain. Such colony locations have often been cited as characteristic of the species (Aguirre 1995, Macdonald *et al.* 2002, Kendall *et al.* 2003, Naveen & Lynch 2011). Colonies were typically located near cliffs, offering protection and drainage benefits, with solid rock substrates reducing risks from stagnant water and snow, and providing suitable materials for nest building. Cliff sites also limit competition from heavier and less agile Adélie and Gentoo Penguins (Volkman & Trivelpiece 1981, Jabłoński 1984b).

A broader modelling approach is needed to understand the environmental drivers of nesting site selection in penguins and other colonial birds. Techniques such as generalized linear models and generalized additive models, linking nest occurrence to multiple habitat features, offer valuable insights. Holistic analyses indicate terrestrial elevation as the most important variable across all three *Pygoscelis* species (Gallagher *et al.* 2025), consistent with findings for flying colonial birds (Momberg *et al.* 2023, Larsen *et al.* 2024). These models surpass traditional three-dimensional mapping methods but require careful variable selection. Previous research shows that demographic changes and intraspecific interactions influence colony fragmentation and predation risk (McDowall & Lynch 2017, 2019). We emphasize the need for further analysis of terrestrial habitats, particularly under climate change. Future studies should apply supervised classification techniques, e.g. terrain classification with Random Forests in the QGIS/EnMapBOX plugin, to predict potential nesting sites probabilistically and examine species-specific preferences. This approach could generalize findings across *Pygoscelis* colonies, explore multi-species dynamics and improve predictive mapping under varying climatic scenarios.

CONCLUSIONS

This study highlights the effectiveness of fixed-wing UAV BVLOS data, GIS tools and high-resolution digital terrain models in analysing nest-site preferences of three *Pygoscelis* penguin species. The minimally intrusive approach of UAV BVLOS surveys – operated at altitudes of 350–500 m a.s.l. and covering single-flight distances up to 320 km – enables large-scale habitat mapping (see also Korczak-Abshire *et al.* 2016, 2019, Dąbski *et al.* 2017, Zmarz *et al.* 2018, 2023) at a resolution higher than satellite imagery. Statistical analyses confirmed nest-site selectivity in *Pygoscelis* penguin species. The integration of cyclical photogrammetric surveys offers potential to monitor long-term ecological changes, while spatial modelling tools may assist in identifying likely rookery locations in newly accessible regions. This quantitative, non-invasive methodology constitutes a valuable tool for defining species-specific ecological requirements and may support future conservation and management strategies. Its efficiency and minimal disturbance make it a promising solution for repeated ecological assessments.

Data were collected at the Henryk Arctowski Polish Antarctic Station. The authors wish to thank the three anonymous reviewers for their valuable contributions, which improved the manuscript.

AUTHOR CONTRIBUTIONS

Małgorzata Korczak-Abshire: Conceptualization; methodology; software; data curation; investigation; validation; formal analysis; supervision; funding acquisition; visualization; project administration; resources; writing – original draft; writing – review and editing. **Katarzyna Ewa Jaworska:** Conceptualization; writing – review and editing; formal analysis; investigation; visualization; methodology. **Piotr Pabjanek:** Conceptualization; methodology; software; validation; writing – review and editing. **Marlena Kycko:** Investigation; software; validation; writing – review and editing; methodology. **Anna Zmarz:** Data curation; formal analysis; funding acquisition; investigation; project administration; resources; software; validation; writing – review and editing; methodology.

CONFLICT OF INTEREST STATEMENT

All authors have no conflicts of interest to declare.

ETHICAL NOTE

None.

FUNDING

The research leading to these results has received funding from the Polish-Norwegian Research Programme operated by the National Centre for Research and Development under the Norwegian Financial Mechanism 2009-2014 in the frame of Project Contract No. 197810.

Data Availability Statement

Data availability statement The archived data are available for use: (1) https://zenodo.org/records/

14614877, (2) https://doi.org/10.5194/isprsarchives-XL-1-W4-189-2015, (3) http://www.add.scar.org/home/add6, (4) https://doi.org/10.1017/S0032247417000055.

REFERENCES

Agisoft. 2015. Agisoft Photoscan 1.2.0. Software, http://download.agisoft.com/photoscan-pro_1_2_4_x64.msi (accessed December 2015)

Aguirre, C.A. 1995. Distribution and abundance of birds at Potter Peninsula, 25 de Mayo. *Mar. Ornithol.* **23**: 23–31.

Ainley, D.G. 2002. *The Adélie Penguin Bellwether of Climate Change*. New York: Columbia University Press.

Baylis, A.M., Crofts, S. & Wolfaardt, A.C. 2013. Population trends of gentoo penguins *Pygoscelis papua* breeding at The Falkland Islands. *Mar. Ornithol.* **41**: 1–5.

Betts, M.G., Hadley, A.S., Rodenhouse, N. & Nocera, J.J. 2008. Social information trumps vegetation structure in breeding-site selection by a migrant songbird. *Proc. R. Soc. B Biol. Sci.* **275**: 2257–2263.

Black, C.E. 2016. A comprehensive review of the phenology of *Pygoscelis* penguins. *Polar Biol.* **39**: 405–432.

Boersma, P.D. 2008. Penguins as marine sentinels. *Bioscience* **58**: 597–607.

Borboroglu, P.G. & Boersma, P.D. 2013. *Penguins: Natural History and Conservation*. Seattle: University of Washington Press.

Chesalin, M., Naveen, R., Lynch, H., Bullock, I., Rider, M., Miller, A., Forrest, S., Dagit, R., Dykyy, I. & Timofeyev, V. 2009. Long-term changes in populations of seabirds on Petermann Island and surrounding islands in Graham Land, Antarctic peninsula. *Mar. Ecol. J.* **8**: 5–13.

Cimino, M.A., Patterson-Fraser, D.L., Stammerjohn, S. & Fraser, W.R. 2019. The interaction between Island geomorphology and environmental parameters drives Adélie penguin breeding phenology on neighboring islands near Palmer Station, Antarctica. *Ecol. Evol.* **9**: 9334–9349.

Colombelli-Négrel, D. & Iasiello, L. 2023. The importance of fine-scale landscape characteristics for habitat selection in penguins. *Biodivers. Conserv.* **32**: 1369–1401.

Convey, P. & Peck, L.S. 2019. Antarctic environmental change and biological responses. *Sci. Adv.* **11**: eaaz0888. www.ipcc.ch/2019/09/25/srocc-press-release/

Dąbski, M., Zmarz, A., Pabjanek, P., Korczak-Abshire, M., Karsznia, I. & Chwedorzewska, K.J. 2017. UAV-based detection and spatial analyses of periglacial landforms on Demay point (King George Island, South Shetland Islands, Antarctica). *Geomorphology* **290**: 29–38.

De Neve, L., Fargallo, J.A., Polo, V., Martín, J. & Soler, M. 2006. Subcolony characteristics and breeding performance in the chinstrap penguin *Pygoscelis antarctica*. *Ardeola* **53**: 19–29.

Dunn, M.J., Jackson, J.A., Adlard, S., Lynnes, A.S., Briggs, D.R., Fox, D. & Waluda, C.M. 2016. Population size and decadal trends of three penguin species nesting at Signy Island, South Orkney Islands. *PLoS One* **11**: e0164025.

Everitt, B.S. 2002. Coefficient of variation. In *The Cambridge Dictionary of Statistics*: 410. Cambridge: Cambridge University Press.

Gallagher, K.L., Herman, R., Walton, K., Dinniman, M.S. & Lynch, H.J. 2025. *Pygoscelis* penguins prefer different oceanographic and terrestrial habitats during the austral summer. *Ecosphere* **16**: e70091.

Gjerdrum, C., Elphick, C.S. & Rubega, M. 2005. Nest site selection and nesting success in saltmarsh breeding sparrows: The importance of Nest habitat, timing, and study site differences. *Condor* **107**(I4): 849–862.

Grohmann, C.H., Smith, M.J. & Riccomini, C. 2011. Multiscale analysis of topographic surface roughness in the Midland Valley, Scotland. *IEEE Trans. Geosci. Remote Sens.* **49**: 1200–1213.

Herman, R., Borowicz, A., Lynch, M., Trathan, P., Hart, T. & Lynch, H. 2020. Update on the global abundance and distribution of breeding gentoo penguins (*Pygoscelis papua*). *Polar Biol.* **43**: 1947–1956.

Hinke, J.T., Polito, M.J., Goebel, M.E., Jarvis, S., Reiss, C.S., Thorrold, S.R., Trivelpiece, W.Z. & Watters, G.M. 2015. Spatial and isotopic niche partitioning during winter in chinstrap and Adélie penguins from the South Shetland Islands. *Ecosphere* **6**: 125–132.

Hinke, J.T., Cossio, A.M., Goebel, M.E., Reiss, C.S., Trivelpiece, W.Z. & Watters, G.M. 2017. Identifying risk: Concurrent overlap of the Antarctic krill fishery with krill-dependent predators in the Scotia Sea. *PLoS One* **12**: 1–24.

Hinke, J.T., Santos, M.M., Korczak-Abshire, M., Milinevsky, G. & Watters, G.M. 2019. Individual variation in migratory movements of chinstrap penguins leads to widespread occupancy of ice-free winter habitats over the continental shelf and deep ocean basins of the Southern Ocean. *PLoS One* **14**: e0226207.

Jabłoński, B. 1984a. Distribution and numbers of penguins in the region of King George Island (South Shetland Islands) in the breeding season 1980/1981. *Pol. Polar Res.* **5**: 17–30.

Jabłoński, B. 1984b. Distribution, numbers and breeding preferences of penguins in the region of the Admiralty Bay (King George Island, South Shetland Islands) in the season 1979/1980. *Pol. Polar Res.* **5**: 5–16.

Jaworska, K. 2016. Związek lokalizacji gniazd pingwinów *Pygoscelis* z cechami rzeźby terenu. MSc thesis, Uniwersytet Warszawski, Warszawa.

Jenson, S.K. & Domingue, J.O. 1988. Extracting topographic structure from digital elevation data for geographic information system analysis. *Photogramm. Eng. Remote Sens.* **54**: 1593–1600.

Jones, J. 2001. Habitat selection studies in avian ecology: A critical review. *Auk* **118**: 557–562.

Kendall, K.A., Ruhl, H.A. & Wilson, R.C. 2003. Distribution and abundance of marine bird and pinniped populations within port Foster, Deception Island, Antarctica. *Deep Sea Res. Part II Top. Stud. Oceanogr.* **50**: 1873–1888.

Kildaw, S.D. 1999. Competitive displacement? An experimental assessment of nest site preferences of cliff-nesting gulls. *Ecology* **80**: 576–586.

Korczak-Abshire, M., Węgrzyn, P.J., Angiel, P.J. & Lisowska, M. 2013. Pygoscelid penguins breeding distribution and population trends at Lions Rump rookery, King George Island. *Pol. Polar Res.* **34**: 87–99.

Korczak-Abshire, M., Kidawa, A., Zmarz, A., Storvold, R., Karlsen, S.R., Rodzewicz, M., Chwedorzewska, K. & Znój, A. 2016. Preliminary study on nesting Adélie penguins disturbance by unmanned aerial vehicles. *CCAMLR Sci.* **23**: 1–16.

Korczak-Abshire, M., Zmarz, A., Rodzewicz, M., Kycko, M., Karsznia, I. & Chwedorzewska, K.J. 2019. Study of fauna population changes on Penguin Island and Turret Point Oasis (King George Island, Antarctica) using an unmanned aerial vehicle. *Polar Biol.* **42**: 217–224.

Korczak-Abshire, M., Hinke, J.T., Milinevsky, G., Juáres, M.A. & Watters, G.M. 2021. Coastal regions of the northern Antarctic peninsula are key for gentoo populations. *Biol. Lett.* **17**: 20200708.

Korne, N., Flemming, S.A., Smith, P.A. & Nol, E. 2020. Applying structure-from-motion habitat reconstruction and GIS terrain analysis to test hypotheses about nest-site selection by shorebirds. *J. Field Ornithol.* **91**: 421–432.

Larsen, G.D., Varga, H.F., Patterson-Fraser, D.L., Johnston, D.W. & Cimino, M.A. 2024. Drone-based monitoring and geomorphology of southern giant petrel nests near Palmer Station, western Antarctic peninsula. *Polar Biol.* **47**: 459–474.

Lee, J.R., Raymond, B., Bracegirdle, T.J., Chadès, I., Fuller, R.A., Shaw, J.D. & Terauds, A. 2017. Climate change drives expansion of Antarctic ice-free habitat. *Nature* **547**: 49–54.

Lishman, G.S. 1985. The comparative breeding biology of Adélie and chinstrap penguins *Pygoscelis adeliae* and *P. antarctica* at Signy Island, South Orkney Islands. *Ibis* **127**: 84–99.

Lynch, H.J. & Larue, M.A. 2014. First global census of the Adélie penguin. *Auk* **131**: 457–466.

Macdonald, J.A., Barton, K.J. & Metcalf, P. 2002. Chinstrap penguins (*Pygoscelis antarctica*) nesting on Sabrina islet, Balleny Islands, Antarctica. *Polar Biol.* **25**: 442–447.

Martin, T.E. 1998. Are microhabitat preferences of coexisting species under selection and adaptive? *Ecology* **79**: 656–670.

Massaro, M., Chardine, J.W. & Jones, I.L. 2001. Relationships between black-legged kittiwake nest-site characteristics and susceptibility to predation by large gulls. *The Condor* **103**: 793–801.

McDowall, P. & Lynch, H.J. 2017. Ultra-fine scale spatially-integrated mapping of habitat and occupancy using structure-from-motion. *PLoS One* **12**: e0166773.

McDowall, P. & Lynch, H.J. 2019. When the "selfish herd" becomes the "frozen herd": Spatial dynamics and population persistence in a colonial seabird. *Ecology* **100**: e02823.

Moczydłowski, E. 1989. Protection of eggs and chicks against flooding as a part of nesting strategy of pygoscelid penguins at King George Island, South Shetlands. *Pol. Polar Res.* **10**: 163–181.

Momberg, M., Ryan, P.G., Hedding, D.W., Schoombie, J., Goddard, K.A., Craig, K.J. & Le Roux, P.C. 2023. Factors determining nest-site selection of surface-nesting seabirds: A case study on the world's largest pelagic bird, the wandering albatross (*Diomedea exulans*). *Ibis* **165**: 190–203.

Müller -Schwarze, D. 1984. The chinstrap penguin. In Müller-Schwarze, D. (ed) *The Behavior of Penguins: Adapted Ice and Tropics*: 95–107. Albany, USA: State University of New York Press.

Mustafa, O. & Pfeifer, C. 2014. Aerial drone based high resolution DSM of three penguin colonies at the South Shetland Islands, Antarctica [Data set]. *Zenodo*. https://doi.org/10.5281/zenodo.14614877

Mustafa, O., Esefeld, J., Grämer, H., Maercker, J., Rümmler, M.-C., Senf, M., Pfeifer, C. & Peter, H.-U. 2017. *Monitoring penguin colonies in the Antarctic using remote sensing data*. Umweltbundesamt. Texte 30/2017. Dessau-Roßlau, Germany.

Myrcha, A., Pietr, S.J. & Tatur, A. 1985. The role of Pygoscelid penguin rookeries in nutrient cycles at Admiralty Bay, King George Island. In Siegfried, W.R., Condy, P.R. & Laws, R.M. (eds) *Antarctic Nutrient Cycles and Food Webs*: 156–162. Berlin: Springer-Verlag.

Myrcha, A., Tatur, A. & del Valle, R. 1987. Numbers of Adélie penguins breeding at Hope Bay and Seymour Island rookeries (West Antarctica) in 1985. *Pol. Polar Res.* **8**: 411–422.

Naveen, R. & Lynch, H. 2011. *Compendium of Antarctic Peninsula Visitor Sites. 3rd Edition*. Chevy Chase, USA: Oceanites, Inc.

Oosthuizen, W.C., Krüger, L., Jouanneau, W. & Lowther, A.D. 2020. Unmanned aerial vehicle (UAV) survey of the Antarctic shag (*Leucocarbo bransfieldensis*) breeding colony at harmony point, Nelson Island, South Shetland Islands. *Polar Biol.* **43**: 187–191.

Patterson, D.L. 2001. *The effects of human activity and environmental variability on long-term changes in Adélie penguin populations at Palmer Station, Antarctica*. PhD thesis, Montana State University Bozeman, Montana.

Patterson, D.L., Easter-Pilcher, A. & Fraser, W. 2003. The effects of human activity and environmental variability on long-term changes in Adélie penguin populations at Palmer Station, Antarctica. In Huiskes, A.H.L., Gieskes, W.W.C., Rozema, J., Schorno, R.M.L., van der Vies, S.M. & Wolff, W.J. (eds) *Antarctic Biology in a Global Context*: 301–307. The Netherlands: Backhuys Publishers.

Pratte, I., Davis, S.E., Maftei, M. & Mallory, M.L. 2016. Aggressive neighbors and dense nesting: Nest site choice and success in high-Arctic common eiders. *Polar Biol.* **39**: 1597–1604.

Pudełko, R., Angiel, P.J., Potocki, M., Jędrejek, A. & Kozak, M. 2018. Fluctuation of glacial retreat rates in the eastern part of Warszawa icefield, King George Island, Antarctica, 1979-2018. *Remote Sens.* **10**: 892.

Quintana, R.D. 2001. Nest-site characteristics of a gentoo penguin *Pygoscelis papua* colony at Cierva Point, Antarctic Peninsula. *Mar. Ornithol.* **29**: 109–112.

Quintana, R.D. & Cirelli, V. 2000. Breeding dynamics of a gentoo penguin *Pygoscelis* papua population at Cierva Point, Antarctic Peninsula. *Mar. Ornithol.* **28**: 29–35.

R Core Team 2024. *R: A Language and Environment for Statistical Computing*. Vienna, Austria: R Foundation for Statistical Computing. Available at: https://www.R-project.org/

Rodzewicz, M., Głowacki, D. & Hajduk, J. 2017. Some dynamic aspects of photogrammetry missions performed by "PW-ZOOM"-the UAV of Warsaw University of Technology. *Arch. Mech. Eng.* **64**: 37–55.

Ropert-Coudert, Y., Kato, A., Meyer, X., Pellé, M., MacIntosh, A.J., Angelier, F., Chastel, O., Widmann, M., Arthur, B.F., Raymond, B. & Raclot, T. 2015. A complete breeding failure in an Adélie penguin colony correlates with unusual and extreme environmental events. *Ecography* **38**: 111–113.

Santa Cruz, F. & Krüger, L. 2023. Breeding population and nesting habitat of skuas in the harmony point Antarctic specially protected area. *Diversity* **15**: 638.

Schmidt, A.E., Ballard, G., Lescroël, A., Dugger, K.M., Jongsomjit, D., Elrod, M.L. & Ainley, D.G. 2021. The influence of subcolony-scale nesting habitat on the reproductive success of Adélie penguins. *Sci. Rep.* **11**: 1–15.

Sierakowski, K., Korczak-Abshire, M. & Jadwiszczak, P. 2017. Changes in bird communities of Admiralty Bay, King George Island (West Antarctic): Insights from monitoring data (1977-1996). *Pol. Polar Res.* **38**: 231–262.

Strycker, N., Wethington, M., Borowicz, A., Forrest, S., Witharana, C., Hart, T. & Lynch, H.J. 2020. A global population assessment of the chinstrap penguin (*Pygoscelis antarctica*). *Sci. Rep.* **10**: 19474.

Trivelpiece, W.Z. & Fraser, W.R. 1996. The breeding biology and distribution of Adélie penguins: Adaptations to environmental variability. In Hofmann, Q.L. & Ross, E.E. (eds) *Foundations for Ecological Research West of the Antarctic Peninsula, Antarctic Research Series*: 273–285. Washington, D.C.: American Geophysical Union. https://doi.org/10.1029/ar070p0273

Trivelpiece, W.Z. & Trivelpiece, S.G. 1990. Courtship period of Adélie, gentoo, and chinstrap penguins. In Davis, L.S. & Darby, J.T. (eds) *Penguin Biology*: 113–127. Amsterdam, Netherlands: Elsevier. https://doi.org/10.1016/b978-0-08-057106-5.50012-7

Trivelpiece, W. & Volkman, N. 1979. Nest-site competition between Adélie and chinstrap penguins: An ecological interpretation. *Auk* **96**: 675–681.

Trivelpiece, W.Z., Trivelpiece, S.G. & Volkman, N.J. 1987. Ecological segregation of Adélie, gentoo, and chinstrap penguins at King George Island, Antarctica. *Ecology* **68**: 351–361.

Volkman, N.J. & Trivelpiece, W. 1981. Nest-site selection among Adélie, chinstrap and gentoo penguins in mixed species rookeries. *Wilson Bull.* **93**: 243–248.

Watters, G.M., Hinke, J.T. & Reiss, C.S. 2020. Long-term observations from Antarctica demonstrate that mismatched scales of fisheries management and predator-prey interaction lead to erroneous conclusions about precaution. *Sci. Rep.* **10**: 5923.

Wickham, H. 2016. *ggplot2: Elegant Graphics for Data Analysis*. New York: Springer.

Williams, T.D. & Rodwell, S. 1992. Annual variation in return rate, mate and Nest-site Fidelity in breeding gentoo and macaroni penguins. *Condor* **94**: 636–645.

Woehler, E.J. 1995. Consumption of Southern Ocean marine resources by penguins. In Dann, P., Norman, I. & Reilly, P. (eds) *The Penguins*: 266–295. Chipping Norton: Surrey Beatty & Sons.

Zaiontz, C. 2016. Real Statistics Using Excel 4.7. Computer Program, www.real-statistics.com (accessed January 2016)

Zmarz, A., Korczak-Abshire, M., Storvold, R., Rodzewicz, M. & Kędzierska, I. 2015. Indicator species population monitoring in Antarctica with UAV. *Int. Arch. Photogramm. Remote Sens. Spatial Inf. Sci.* **40**(1W4): 189–193.

Zmarz, A., Rodzewicz, M., Dąbski, M., Karsznia, I., Korczak-Abshire, M. & Chwedorzewska, K.J. 2018. Application of UAV BVLOS remote sensing data for multi-faceted analysis of Antarctic ecosystem. *Remote Sens. Environ.* **217**: 375–388.

Zmarz, A., Karlsen, S.R., Kycko, M., Korczak-Abshire, M., Gołębiwska, I., Karsznia, I. & Chwedorzewska, K. 2023. BVLOS UAV missions for vegetation mapping in maritime Antarctic. *Front. Environ. Sci.* **11**: 1154115.

Received 25 October 2024;
Revision 11 December 2025;
revision accepted 17 December 2025.
Associate Editor: Richard Phillips.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Figure S1 Breeding population sizes, expressed as the number of nests, of the three study species on King George Island.