



# Human infrastructures correspond to higher Adélie penguin breeding success and growth rate

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## Abstract

Anthropogenic activities generate increasing disturbance in wildlife especially in extreme environments where species have to cope with rapid environmental changes. In Antarctica, while studies on human disturbance have mostly focused on stress response through physiological and behavioral changes, local variability in population dynamics has been addressed more scarcely. In addition, the mechanisms by which breeding communities are affected around research stations remain unclear. Our study aims at pointing out the fine-scale impact of human infrastructures on the spatial variability in Adélie penguin (*Pygoscelis adeliae*) colonies dynamics. Taking 24 years of population monitoring, we modeled colony breeding success and growth rate in response to both anthropic and land-based environmental variables. Building density around colonies was the second most important variable explaining spatial variability in breeding success after distance from skua nests, the main predators of penguins on land. Building density was positively associated with penguins breeding success. We discuss how buildings may protect penguins from avian predation and environmental conditions. The drivers of colony growth rate included topographical variables and the distance to human infrastructures. A strong correlation between 1-year lagged growth rate and colony breeding success was coherent with the use of public information by penguins to select their initial breeding site. Overall, our study brings new insights about the relative contribution and ecological implications of human presence on the local population dynamics of a sentinel species in Antarctica.

**Keywords** *Pygoscelis adeliae* · Antarctica · Population monitoring · Human disturbance · Population dynamics · Breeding habitat quality

## Introduction

Anthropogenic perturbations are durably modifying geochemical cycles and altering environmental features as never before during the Holocene (Waters et al. 2016). The

Anthropocene is characterized by an accumulation of climate anomalies associated with an increased extinction rates for all groups of vertebrate (Ceballos et al. 2015), resulting from the overexploitation of natural resources and alterations to the habitat (Horváth et al. 2019). Marine ecosystems are no exception to human-induced habitat transformations: oceans are subjected to various pollutions, either chemical, e.g., through microplastics (Roy et al. 2022) and pharmaceuticals (Gaw et al. 2014), or physical, e.g., by noise generated by ship propellers (Erbe et al. 2019), acoustic and magnetic disturbances from offshore wind farms (Bergström et al. 2014). Moreover, local human disturbances are concomitant with rapid transformations in ocean dynamics induced by climate change that may have cumulative effects on wildlife, which need to be assessed and characterized.

Polar regions are particularly prone to rapid environmental changes even under small climate fluctuations: changes in sea-ice seasonality (Cavaliere and Parkinson 2012) and

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Sizing the anthropic impact on Antarctic wildlife is a priority of managing committees. We report a long-term effect of infrastructures on a key species. This may help Antarctic conservation planning.

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increasing areas of ice-free land in summer (Post et al. 2019). In Polar Regions such as Antarctica, the physical environment is changing rapidly, both at sea (Purich et al. 2016; Lee et al. 2017b; Eayrs et al. 2021) and on land (Lee et al. 2017a). Expanding coastal ice-free patches—which host the reproduction sites of most Antarctic-breeding seabirds—potentially uncovers new breeding sites and pushes the latitudinal distribution of subantarctic species southward (Convey and Peck 2019; Gutt et al. 2021). In some areas, these abiotic changes are aggravated by intense local human pressures e.g. industrial fisheries, growing tourism (McCarthy et al. 2019) and research activities (Perterra et al. 2017). Because of this, studying the long-term impact of human presence on Antarctic wildlife has become a major topic both for providing guidelines for conservation (Coetzee et al. 2017) and for unraveling species responses to climate change from anthropogenic stress (Bricher et al. 2008).

To disentangle human-induced effects from broader climate changes on ecosystems, insights can be gained from areas subjected to a gradient of human activities. Isolated research stations such as Dumont d'Urville in Adélie land (location 66°39'47" S and 140°00'10" E), offer such variability in terms of human impact. Indeed, infrastructures of the station are grouped and closely surrounded by breeding bird colonies whose distance to the buildings range from a few meters to several hundreds (photos in the Fig. 1). In addition to this particular configuration, the station benefits from long-term population monitoring of local bird species (Barbraud et al. 2020). These species are considered relevant bioindicators of changes in Antarctic ecosystems. However, they exhibit different levels of sensitivity to human presence and habitat transformations in terms of demography (Micol and Jouventin 2001). Sensitive populations like the Southern giant petrel (*Macronectes giganteus*) decreased by 43% between 1985 and 1999, while other species significantly increased over the same period, notably the Adélie penguin (*Pygoscelis adeliae*)—65% population increase 1985–2018; (Barbraud et al. 2020)—and the South polar skua (*Stercorarius maccormicki*, hereafter named skua)—61% population increase (Pacoureaux et al. 2019b). For Adélie penguins in particular, contrasted results have been reported elsewhere in response to human proximity (Carlini et al. 2007; Bricher et al. 2008). Station proximity was mostly associated with decreasing population (Bricher et al. 2008), and lower breeding success (Woehler et al. 1994). However, the influence of station proximity seems often outweighed by environmental variability (Carlini et al. 2007) and no clear long-term effect of stations on breeding Adélie penguins populations have been reported yet. At the individual scale, however, Adélie penguins strongly react to human approach and handling with immediate physiological responses including increased heart rate (Culik et al. 1990) and stress-hormone release (Cockrem et al. 2008). Hence, between the whole population

dynamics and the individual physiological responses, insights may come from studying the intermediate colony-scale response to long-term human presence. Indeed, Adélie penguin populations are organized into spatially individualized colonies—of at least three and up to several thousands pairs (Ainley 2002)—whose local population dynamics are influenced by the surrounding environmental conditions (Schmidt et al. 2021). In the context of the research station, if infrastructures negatively influence breeding penguins, then colony-scale breeding success and population dynamics should be affected with deleterious effects.

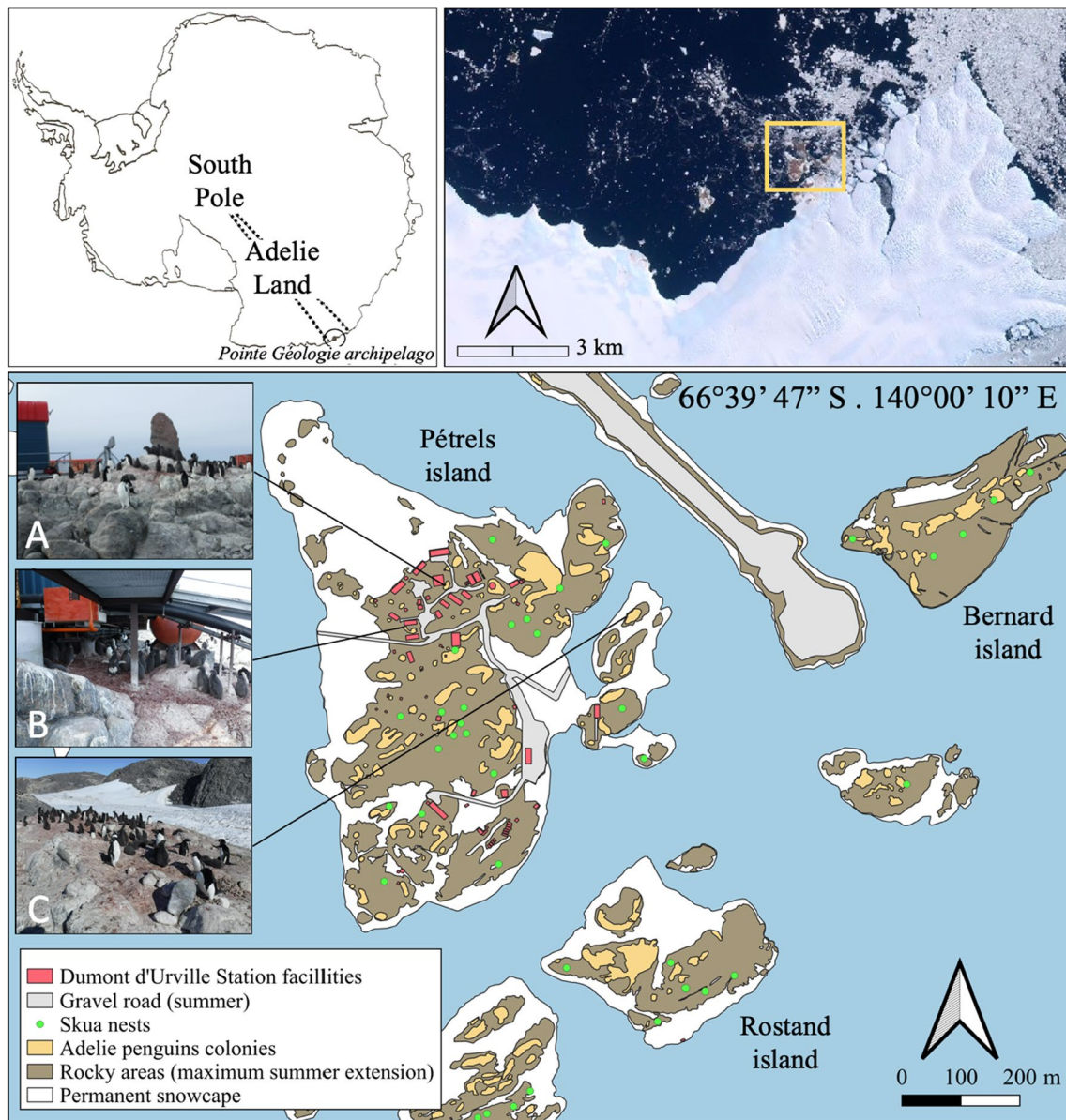
The spatial drivers of breeding success of two Adélie penguin colonies were recently analyzed at the colony scale in Ross island (Schmidt et al. 2021). Smaller perimeter-to-area ratio of the colonies—likely reflecting nest predation by skua at the edge of the groups—shallower slopes and higher elevation were among the main drivers of colony breeding success (Schmidt et al. 2021). In the present study, we integrate variables derived from the Dumont d'Urville infrastructures and other local environmental characteristics to predict Adélie penguins colony breeding success. In the particular context of human facilities around penguin colonies, we hypothesize that (1) a high colony breeding success would be associated with a low human footprint—i.e., longer distance between colonies and infrastructures or lower infrastructures density around the colonies. Moreover, we hypothesize that (2) a negative impact of infrastructures on breeding success may also influence long-term colony demography. Hence, the growth rate of colonies in the vicinity of the infrastructures should be lower than the one of colonies situated far from infrastructures.

## Materials and methods

### Study area and population monitoring

Demographic data were collected in Pointe Géologie archipelago, Adélie Land, Antarctica from 1998 to 2021 (i.e., breeding cycles 1998/1999, hereafter 1998 and so on). The study area encompasses Pétrels island—where the Dumont d'Urville research station is built—and the two neighboring islands Bernard and Rostand classified as Antarctic Specially Protected Area ASPA-120 (Fig. 1). The ASPA-120 remains free of major human infrastructures and access is restricted to authorized scientific monitoring only.

Adult Adélie penguins mate mid-October and usually lay two eggs. Their breeding cycle spans through late-February when the last chicks fledge. Population monitoring occurs twice for each reproductive cycle  $i$ . Breeding pairs ( $A_i$ ) are ground counted mid-November of year  $i$  and fledged chicks are counted (mix of aerial photography and ground counting depending on weather conditions and location)



**Fig. 1** Study area in the Pointe Géologie Archipelago, Adélie land, Antarctica. Satellite caption shows the area of the Pointe Géologie archipelago near the coast of Adélie land and the Astrolabe glacier to the East (Copernicus Sentinel-2 satellite snapshot taken on January 19th 2021, processed by ESA). The study area spans over three islands of the Pointe Géologie archipelago: Pétrels, Bernard, and Rostand islands. Yellow polygons indicate Adélie penguins colonies

counted annually for demographic monitoring. Red polygons represent station buildings. Green dots are skua nest locations. Pictures on the left depict different penguin colonies configurations regarding station's infrastructures: **A** colony located in the middle of the station; **B** colony located under a building; **C** colony located outside the core station

mid-February ( $F_{i+1}$ ) of year  $i + 1$  (see Barbraud et al. 2020 for methodological details). The breeding success of each colony (i.e., the number of chicks fledged per pair) for cycle  $i$  was calculated as the ratio  $F_{i+1}/A_i$ .

We defined penguin colonies as individualized groups of at least three breeding pairs nesting on ice-free rocky areas (Ainley 2002; Schmidt et al. 2021). The study colonies remained spatially stable probably in part because of the

penguin philopatry at the colony scale (Ainley and DeMaster 1980; Ainley 2002; Cimino et al. 2016) and adult nest-site fidelity (Schmidt et al. 2021) (Fig. 1). If two or more nearby colonies were counted together at least once, then we merged them through the entire time-series. We obtained a total of 83 colonies on the three islands. We mapped each colony using georeferenced aerial pictures (taken during the breeding cycle 2016/2017) imported in the Geographic



Information System software QGIS (2019). Each of the 83 colonies has not been counted every year, either because of technical limitations or because of the absence of breeding penguins on each colony on that year. A detailed mapping of the available data is provided in the Online Resource 2 with the number of colonies counted for each year. Three breeding cycles have been discarded due to missing data (1999/2000) or zero-chick survival (2013/2014 and 2016/2017, Barbraud et al. 2015; Ropert-Coudert et al. 2018).

We calculated the growth rate  $\lambda$  of each colony  $s$  with the equation (Eq. 1) linking the number of breeding pairs for the two extreme years of the time-series; 1998 and 2021. Out of the 83 colonies, only 70 were counted in both 1998 and 2021 (a map of observed colonies is provided in Fig. 4, panel (b))

$$\lambda(s) = \frac{A_{i+n}(s)^{1/n}}{A_i(s)} \quad (1)$$

## Colony characteristics

All covariate maps and distributions are provided in the Online Resource 3. Explanatory covariates included five topography-derived variables (elevation, slope, aspect, windshelter index, and topography wetness index), one related to predation pressure (distance to the nearest skua nest), two derived from human infrastructures (distance to the nearest building and building density), and two intrinsic to the colony (surface area and perimeter-to-area ratio).

### Topographic covariates

Topography is a major factor affecting nest selection in Adélie penguins (Ainley 2002). Following (Schmidt et al. 2021), we selected a set of five environmental covariates reflecting colony steepness and exposure to meteorological stressors like heat, wind, and snow accumulation. This includes elevation, slope, aspect, windshelter index and topography wetness index (TWID). Slope may affect colony size, snow accumulation, and the probability of eggs rolling off the nest (De Neve et al. 2006). Wind may increase wind chill in exposed areas or may trigger snowdrift formation in sheltered areas. Excessive snow accumulation is detrimental to egg development and chicks by burying nests under snowdrifts. Moreover, melting snow chills eggs and chicks and can even drown them (Bricher et al. 2008; Fraser et al. 2013). To identify areas of higher risk of snow- and flood-related nests failures, we calculated a topographic-derived windshelter index and a topographic wetness index.

To calculate the topographic characteristics of each colony, we built environmental covariate rasters in R from a Digital Elevation Model (DEM)—the Reference Elevation Model of Antarctica (REMA—Polar Geospatial Center)

(Howat et al. 2019). The tile containing the Pointe Géologie archipelago (mosaic tile 11\_47\_8m with 8 m of lateral resolution and 1 m vertical resolution) was downloaded from the REMA website (Polar Geospatial Center and University of Minnesota).

We derived an elevation raster in R from the raw DEM data. We calculated slopes and aspects (i.e., the direction physical slopes faces in degrees related to geographic North) by processing the DEM data with the starsExtra package (v.0.2.7, Dorman 2024). Aspect calculation from DEM was corrected for the polar inaccuracy between grid north and geographic north as described in (Moret and Huerta 2007).

To take into account the effect of snow on colonies (Bricher et al. 2008; Schmidt et al. 2021), we calculated a windshelter index (wind.shelter function, RSAGA package v. 1.3.0, Winstral et al. 2002; Brenning 2008). The function requires the elevation raster and is called by a focal function containing user-supplied wind angle and radius. We chose a wind angle of 140° (S-SE) which is the dominant direction of the katabatic wind blowing on the archipelago (König-Langlo et al. 1998). We applied a tolerance angle of 22.5° to allow for a wind direction blowing from the whole continental coastline with an angular range from 117.5° (South-East) to 162.5° (South). The maximum search radius of the rolling-window was fixed to 100 m. Higher wind shelter index means higher snowdrift formation risk, and negative index values correspond to exposed wind areas where snow accumulates less.

Terrain wetness and wet conditions are major factors influencing penguin chicks survival during the breeding season (De Neve et al. 2006; Ropert-Coudert et al. 2015). To account for flood risk in colonies, we calculated a topographic wetness index downslope using the whiteboxTools hydrology package (v2.1.5, Wu and Brown 2022). The index calculates how likely a cell is to be wet according to its slope and the weighted slope accumulation of the surrounding cells flowing toward.

### Predation and infrastructure covariates

The main predator of penguin chicks on land are skuas whose predation is known to influence colony breeding success especially on the edges (Emslie et al. 1995; Wilson et al. 2017; Pacoureaux et al. 2019b). At Pointe Géologie skua territories, which generally include Adélie penguin colonies in their perimeter, are visually identified every year for population monitoring (Pacoureaux et al. 2019a). To take predation risk on colonies into account, we mapped all skua territories found repeatedly across years and derived a raster of distance to the nearest territory.

To dissect the influence of long-term human proximity on colony dynamics, we used infrastructures as a proxy of chronic human disturbance on Adélie penguins. We derived

infrastructure layers from the polygons of buildings that we generated from georeferenced aerial images taken during the breeding season 2016/2017 on Pétrels island, similarly to the spatial layer of Adélie penguin colonies. We then selected the buildings considered to generate most human traffic and noise (i.e., living buildings, dormitories, offices, garage, power plant, and helicopter platforms) and excluded passive buildings used for storage. We rasterized each building polygon and derived a raster of distance to the nearest building for the three islands. For building density, we generated 40-m buffers around each building and then summed the raster layers outputs to generate a building density map.

Finally, we characterized each colony by its area and perimeter calculated in R Core Team (2023) with the *sf* (v. 1.0-7, Pebesma et al. 2024) and *lwgeom* (v. 0.2-8, Pebesma 2018) packages, respectively. Perimeter-to-area ratio is an indicator of edge nests proportion in new or growing colonies (Schmidt et al. 2021). Distributions of area and perimeter-to-area values are displayed in the Online Resource 3.

## Statistical modeling

To account for repeated data per colony, we modeled spatial variations in breeding success using a Generalized Additive Mixed Models approach (GAMM, R package *mgcv* v1.8-39, Wood 2017). Populations' dynamics were modeled with a Generalized Additive Model (GAM, R package *mgcv* v1.8-39, Wood 2017).

Colony breeding success varies temporally due to prey availability and meteorological conditions. To compare the relative breeding success between colonies, we controlled for colony-scale temporal variations by subtracting annual mean breeding success of all colonies from the annual breeding success per colony. We used the residual mean annual breeding success as a measure of the spatial variability in breeding success between colonies (Schmidt et al. 2021). For population dynamics, we used the growth rate  $\lambda$  of each colony through the whole study period as a response variable.

To compare the magnitude of their effects on the response variables, we standardized all explanatory covariates, so that their mean is equal to zero and standard deviation equal to one. All covariates were tested for the absence of collinearity with a Variance Inflation Factor inferior to 2 (*usdm* package v1.1-18, Naimi et al. 2014). We used the *gam* function from the *mgcv* package (Wood 2017) fitted with maximum likelihood and with shrinkable thin-plate regression splines. Due to its circular values, we fitted the aspect covariate with a cyclic cubic regression spline ( $-80=180$ ). We used Gaussian family distributions for all models and we limited the basis dimension to  $k=4$ . Because the models for colony breeding success are based on repeated data, we included a random effect of colony identity in the corresponding GAMMs.

We allowed automated model selection by specifying shrinkage smoothers in the *gam* formula (Marra and Wood 2011). Shrinked splines were then removed from the model formula. Finally, we compared the different model fits based on the lowest Akaike Information Criterion (AIC) (for the growth rate model, we used the AICc which corrects for small sized samples;  $n/df < 40$ , Burnham et al. 2010). We were able to obtain one best model for each response variable that we tested for residual distribution and spatial autocorrelation with Moran's *I* test (*spdep* package v1.2-4, Bivand 2022). To assess the predictors' importance in the top-selected models, we removed each predictor at a time and calculated the AIC weight of the resulting model. The Relative Variable Importance (RVI) was calculated by summing AIC weights across all models in the set where the variable occurs (Burnham et al. 2010). We generated prediction maps for colony residual breeding success and growth rate using the top-selected models with the covariate layers.

To really test the effect of infrastructures, we compared our top-selected models to an infrastructure-only model and an environmental-variables-only model. All models were ranked by AIC to evaluate their relative performance.

At the annual scale, we tested for lag-correlations between mean annual breeding success and mean annual growth rate. The growth rate of each colony has been calculated for each year and then smoothed through time by subtracting the annual mean growth rate for all colonies on the three islands from the annual growth rate of each colony. The mean annual breeding success of each colony was then correlated with the year lags of their mean annual growth rate. Both variables were corrected for temporal variability to infer spatially influenced mechanisms of breeding site selection.

## Results

### Breeding success and population dynamics

Contrary to the trend of increasing population at the regional scale reported between 1985 and 2018 (Barbraud et al 2020), the number of nests per colony in the study area remained largely stable throughout the 24-year time-series with a right-skewed distribution and a median number of 162 nests per colony (Q1: 66, Q3: 340, calculated across all years and colonies simultaneously; Online Resource 1, panel (a)). Mean breeding success (i.e., chicks per penguin pair) and productivity (i.e., chicks per colony) were  $0.8 \pm 0.4$  and  $258 \pm 454$ , respectively and varied through time (calculated across all years and colonies simultaneously; Online Resource 1, panel (b) and (c)). Temporal variations in breeding success were correctly smoothed by the mean annual

breeding success of each colony (Online Resource 1, panel (d)).

## Spatial modeling

### Colony breeding success

Infrastructures-only and environmental-variables-only models showed similar adjusted  $R^2$  and overall deviance explained (respectively, 0.116 and 0.118 adjusted  $R^2$ , 14.8% and 14.7% deviance explained, see Table 1) but were not competitive with the top-selected model ( $\Delta\text{AIC} > 2$ ). The top-selected model (m1) included a set of environmental covariates (aspect, Topography Wetness Index Downslope (TWID), windshelter index, perimeter-to-area ratio, and skua nest distance) and building density. The adjusted  $R^2$  and overall deviance explained of m1 were, respectively, 0.115 and 13.8%. Model residuals were randomly distributed around zero and showed no spatial autocorrelations (Moran I statistic standard deviate =  $-0.499$ ,  $p$  value = 0.69). m1 summary is available in the Online Resource 4, Table S1.

The correlation between m1-predicted and observed values in residual breeding success was  $r = 0.38$  (Pearson correlation,  $p$  value  $< 0.001$ ). Distance to the nearest skua nest was the most important covariate according to Relative Variable Importance rank (see RVI in Table 2). The modeled relationship between skua nest distance and residual breeding success was sigmoidal; encompassing zero effect between zero and 100 m, then positive (Fig. 2), indicating that residual breeding success was higher when skua nests were situated  $> 100$  m away from the colonies. Building density was the second most important covariate selected. Colony residual breeding success increased linearly with increasing building density. Windshelter index and perimeter-to-area ratio were, respectively, the third and fourth most important covariates both with a decreasing linear

**Table 2** Relative variable importance (RVI) of the top ranked model explaining variations in colony residual breeding success

Residual breeding success model (m1)				
Term removed	AIC	$\Delta\text{AIC}$	Weight	RVI
None	112.7			
(-skua)	122.2	9.5	0.01	1.48
(-building_density)	120.9	8.2	0.02	1.47
(-windshelter)	115.6	2.9	0.23	1.25
(-perimeter_to_area)	115.1	2.4	0.30	1.18
(-TWID)	115.0	2.3	0.32	1.17
(-aspect)	113.7	1.0	0.61	0.88

AIC corresponds to the AIC of the model once the variable is removed

$\Delta\text{AIC}$  is the difference between the AIC of the top model and the model with the removed variable. RVI is calculated by summing the AIC weights across all the models where the removed variable is present

relationship with residual breeding success. Other selected covariates included topography wetness index with a positive relationship and aspect, for which colony breeding success peaked around  $-75^\circ$  (slopes facing North-West).

The prediction map for colony residual breeding success revealed below average breeding success near the shores and away from the station. Above-average breeding success colonies were concentrated around the infrastructures of the station (Fig. 3).

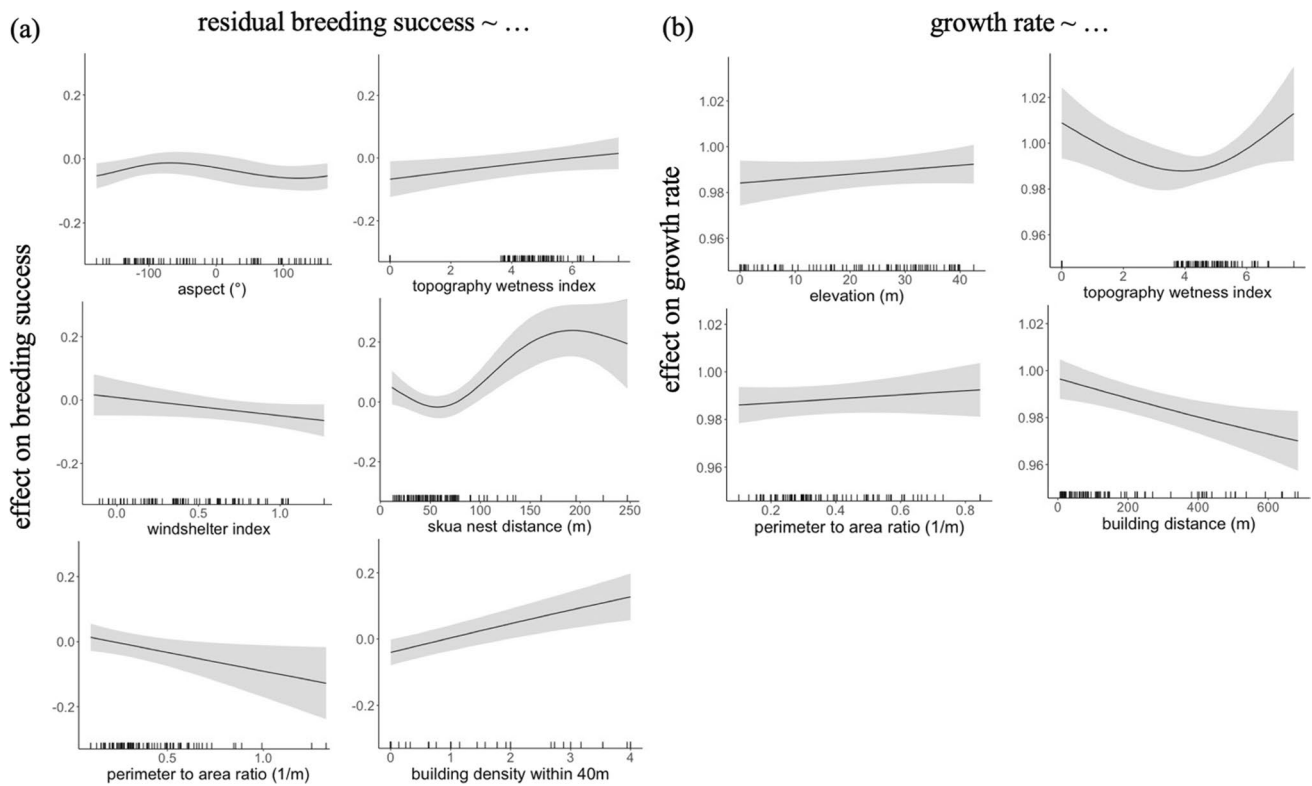
### Growth rate

For growth rate, infrastructure-only and environmental-covariates-only models were not competitive with the top-selected model ( $\Delta\text{AIC} > 2$ , see Table 3). The top-selected model (m4) found no effect for most covariates but elevation, topography wetness index, building distance, and perimeter-to-area ratio. m4 adjusted  $R^2$  and

**Table 1** Generalized additive mixed models used to explain spatial variations in breeding success of Adélie penguin colonies with the residual mean annual breeding success as a response variable

Formula	Description	LogLik	AIC	Delta AIC	df	Weight	$n$	$R^2$ (adjusted)	% Deviance explained
m1: aspect + TWID + windshelter + perimeter_to_area + skua_distance + building_density + (colony as random)	Best model after covariates selection	-18.0	112.7	0.0	38.3	1.000	1431	0.115	13.8%
m2: elevation + slope + aspect + TWID + windshelter + area + perimeter_to_area + skua_distance + (colony as random)	Environmental variables only	-10.6	118.8	6.1	48.8	0.047	1431	0.118	14.7%
m3: building_distance + building_density + (colony as random)	Infrastructures only	-9.4	126.1	13.4	53.7	0.001	1431	0.116	14.8%

Models were compared by AIC, m1 being the best model after covariates selection. m2 included all environmental covariates listed below. m3 included all infrastructure covariates. All models described below included a random effect on colonies due to repeated data per colony across multiple years



**Fig. 2** Predicted relationships between response and explanatory variables. Grey shades correspond to the 95% confidence interval of the prediction. **a** Predicted relationships for the model explaining spatial

variations in colony residual breeding success. **b** Predicted relationships for the model explaining growth rate spatial variations

deviance explained were, respectively, 0.308 and 34.8%. Model residuals were randomly distributed around zero and showed no spatial autocorrelations (Moran I statistic standard deviate = 0.320,  $p$  value = 0.375). m4 summary is available in the Online Resource 4, Table S2.

Correlation between predicted and observed values in colonies growth rate was  $r = 0.59$  (Pearson correlation,  $p$  value < 0.001). The most important variable in the model was the distance to buildings (see Table 4 for RVI) with growth rate linearly decreasing with infrastructures distance (Fig. 2). Topography wetness index was the second most important variable with a U-shaped relationship largely encompassing one (no change in population dynamics). Growth rate also slightly increased with elevation and perimeter-to-area ratio.

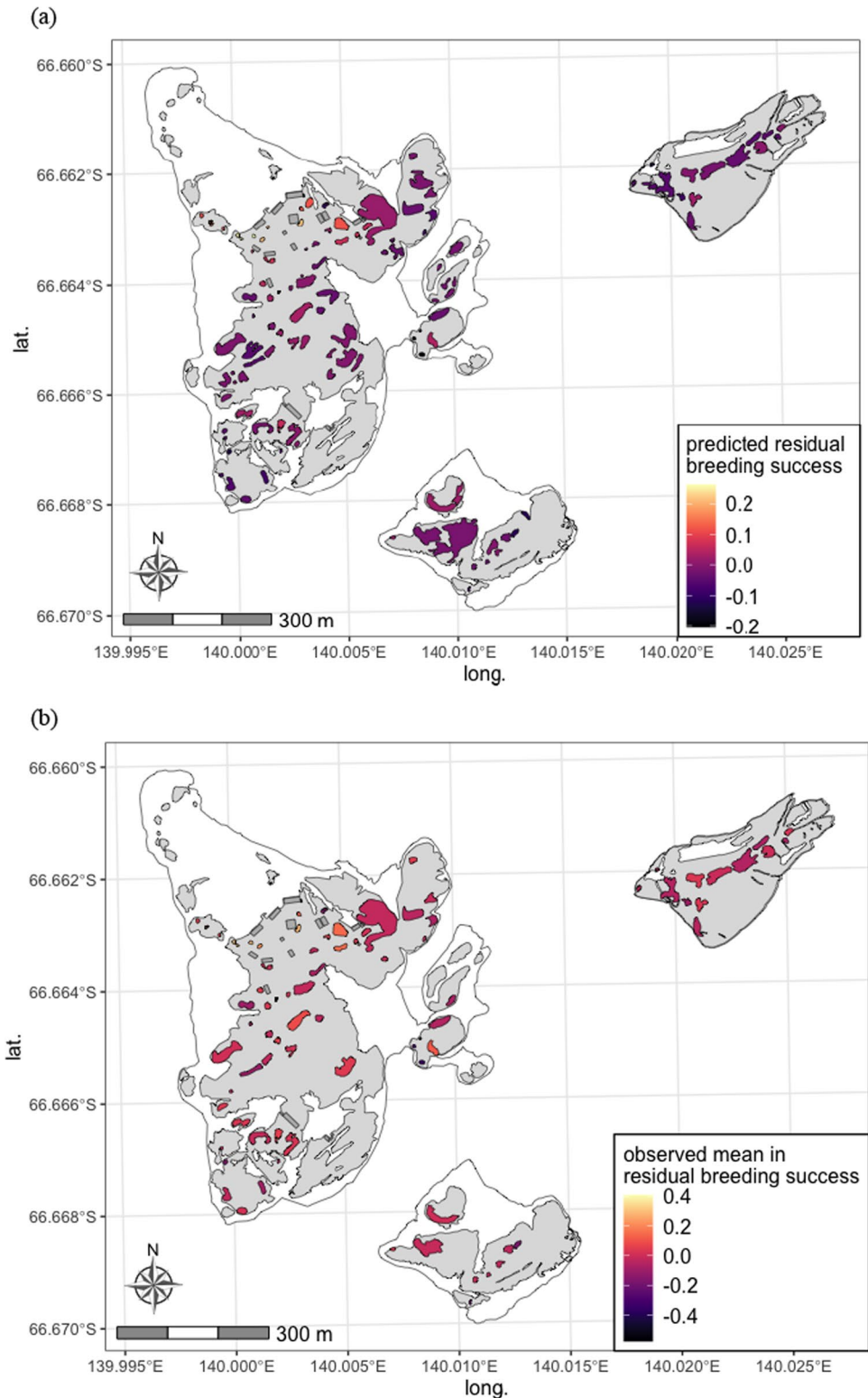
The prediction map for colony growth rate showed increasing population (i.e., growth rate above one) in areas situated close to buildings (Fig. 4). Importantly, colony growth rate mainly increased on the Pétrels Island, while the colony population sizes of the two other islands rather decreased.

### Relationships between population parameters

Predicted values of colony breeding success and growth rate were found to be weakly but significantly correlated (Pearson's correlation  $r = 0.13$ ,  $p$  value < 0.001).

At the annual scale, mean annual breeding success correlated significantly with 3-year lags in mean annual growth rate (Online Resource 7). The first correlation happened at 0-year lag and was negative, meaning that residual breeding success was higher when the annual growth rate was low ( $r = -0.345$ ,  $p$  value < 0.001 =  $6.85e-30$ ). The second correlation was positive at a year lag of one ( $r = 0.375$ ,  $p$  value < 0.001). The third correlation was slightly negative at 2-year lag ( $r = -0.073$ ,  $p$  value = 0.039). Subsequent years seemed to propagate a sigmoid-like relationship between the residuals but with no significant correlation coefficients.

**Fig. 3** Prediction map for colony residual breeding success. Buildings in grey. **a** Positive values indicate above average breeding success, and negative values are below average breeding success areas. **b** Map showing the observed residual breeding success averaged between 1998 and 2021



## Discussion

This study aimed at disentangling the relative contributions of long-term human disturbance and other land-based environmental drivers to Adélie penguins' colonies population

dynamics. We used human infrastructure variables together with topographic-derived covariates to model spatial variability in colony breeding success and growth rate. Contrary to our predictions, infrastructure density was positively associated with colony breeding success, and proximity



**Table 3** Generalized additive models used to explain spatial variations in Adélie penguin colonies growth rate

Formula	Description	LogLik	AIC	Delta AIC	df	Weight	n	R <sup>2</sup> (adjusted)	% deviance explained
m4: elevation + TWID + perimeter_to_area + building_distance	Best model after covariates selection	179.4	−344.9	0.0	7.0	1.000	70	0.308	34.8%
m5: elevation + slope + aspect + TWID + windshelter + area + perimeter_to_area + skua_distance	Environmental variables only	176.8	−341.9	3.0	6.8	0.223	70	0.256	29.7%
m6: ~building_distance + building_density	Infrastructures only	173.0	−339.9	5.0	3.0	0.082	70	0.204	21.6%

Models were ranked by AIC; m4 being the best model after covariates selection. m5 included all environmental covariates and m6 included all infrastructure covariates

**Table 4** Relative variable importance (RVI) of the top ranked model explaining variations in colony growth rate

Growth rate model (m4)				
Term removed	AIC	ΔAIC	Weight	RVI
None	−344.8			
(-building_distance)	−339.2	5.6	0.06	1.65
(-TWID)	−340.6	4.2	0.12	1.59
(-elevation)	−344.0	0.8	0.67	1.04
(-perimeter_to_area)	−345.1	0.3	0.86	0.85

AIC corresponds to the AIC of the model once the variable is removed

ΔAIC is the difference between the AIC of the top model and the model with the removed variable. RVI is calculated by summing the AIC weights across all the models where the removed variable is present

of colonies to infrastructures was associated with higher growth rate.

One can propose that infrastructures could be used as a proxy of chronic human disturbance. This temporally integrated disturbance differs from other disturbance types reported in the literature—such as pedestrian approach, handling of penguins or vehicle operations—which trigger acute physiological and behavioral stress responses in wildlife (Coetzee and Chown 2016). Multiple studies proved human activities around penguins to trigger physiological stress responses [such as accelerated heart rate and increased energy expenditure (Culik et al. 1990), glucocorticoid release—especially upon capture (Cockrem et al. 2008)—and shorter telomeres in chicks from disturbed versus undisturbed areas (Caccavo et al. 2021)]. How these physiological responses translate into population dynamics remains unclear. In a previous study, experimental disturbance (nest checking and simulated recreational visits by tourists) both significantly decreased hatching success and chick survival (Giese 1996). On a wider scale, the effect of aggregated human activities between areas of high and low disturbance has been assessed in Adélie penguin population trends in the

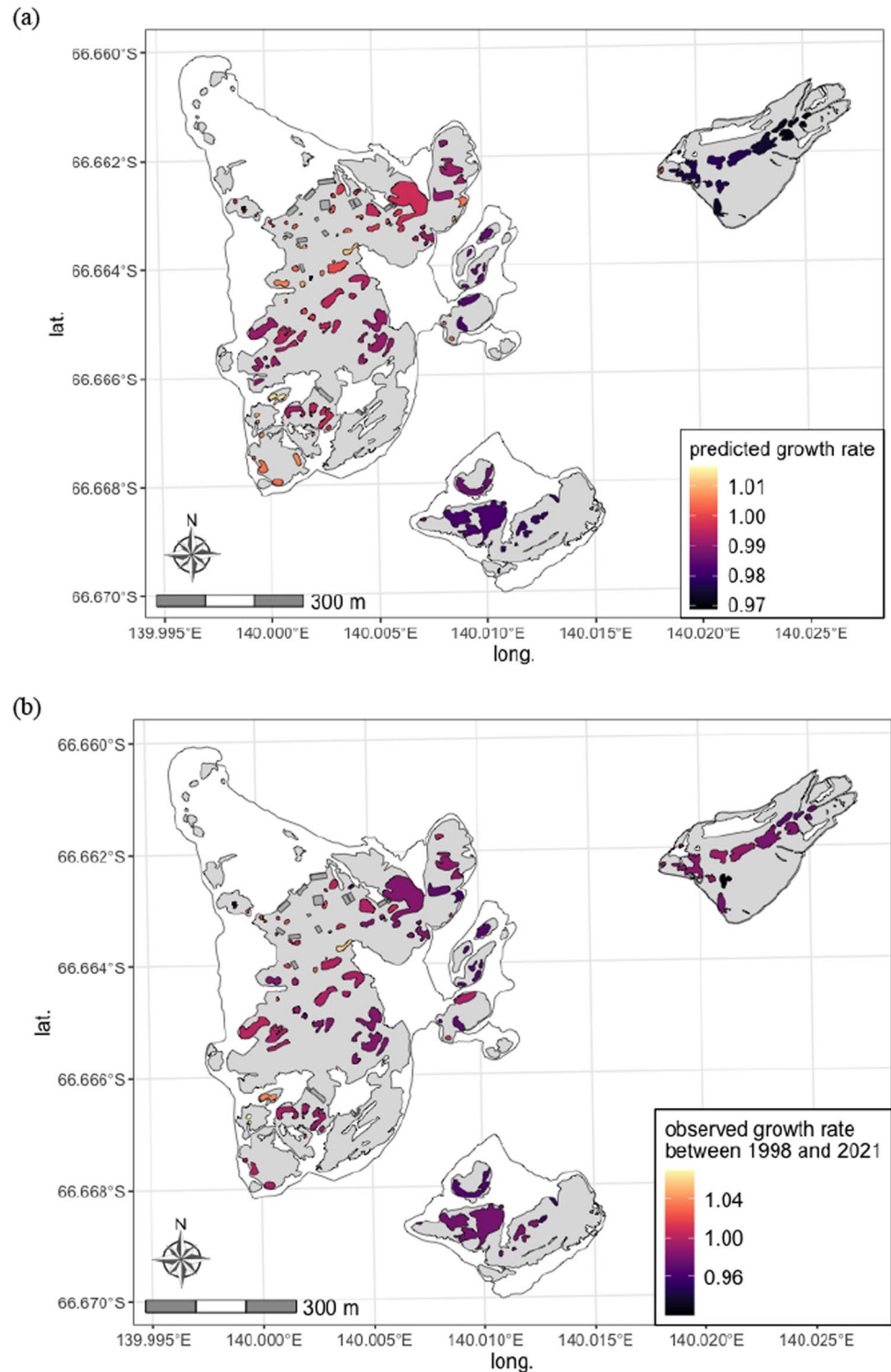
Antarctic Peninsula with no significant differences found in breeding success except in 1996/1997 when breeding success was higher in high human disturbance areas (Carlini et al. 2007). Our results show that, over a long period (24 years), the proximity of human infrastructures was not deleterious to Adélie penguin breeding success and growth rate at the colony scale.

According to Schmidt et al. (2021), the spatial quality of the colony (termed ‘subcolony’ in the paper) was reflected by its relative performances compared to the rest of the study population (termed ‘colony’ in the paper). Our results suggest that colony quality was higher for those colonies located where both building density and breeding success were higher. However, breeding success is only one of the demographic parameters contributing to the growth rate, and other demographic parameters may co-vary negatively with breeding success. Comparing our two models of breeding success and growth rate may then help characterizing more accurately the drivers of colony quality around the station.

However, the exact mechanisms by which human infrastructures may favor breeding success and growth rate of colonies remain unclear. Indeed, colonies located in the vicinity of buildings are experiencing regular and intense disturbances through noise, vibrations, or human and vehicle approaches. Yet, in the longer time scale, the deleterious effects of human presence on penguins may be balanced through selective advantages related to disrupted predation, favorable micro-environment, or behavioral selection as discussed below.

First, skua predation is a major driver of colony breeding success. Indeed, distance to the nearest skua nest was the most influential variable explaining breeding success. Skuas defend foraging territories around their nest, so colonies located close to skua nests are more prone to regular predation attempts on eggs and chicks (Pacoureaux et al. 2019b; Schmidt et al. 2021). Yet, skua nest distance is only a proxy of skua predation and its importance may vary between locations (Schmidt et al. 2021). Indeed, even colonies outside of skua nest territories may experience avian

**Fig. 4** Prediction map for growth rate. Buildings in grey. **a** Values above one correspond to areas of growing population, while values below one indicate contracting population. **b** Map showing the observed residual growth rate for colonies counted both in 1998 and 2021



predation by breeding or non-breeding skuas. Predation pressure increases with skua abundance relative to the number of Adélie nests (Wilson et al. 2017). In our study area, the relatively low Skua abundance (32 skua pairs compared to ~19,000 penguin nests or 0.002 skua pairs per penguin pairs) may explain the importance of skua nest distance in

the predation risk experienced by penguins. Another proxy of predation selected both in Schmidt et al. 2021 and in our own model is the colony perimeter-to-area ratio. This ratio is related to predation risk, because skuas mainly attack nests located at the edge of the colonies (Taylor 2008). A higher perimeter-to-area ratio means a higher proportion of

edge nests which, therefore, results in lower colony breeding success. In this context, the effect of infrastructures could disrupt predation risk by skuas and thus contribute to increased breeding success. A similar mechanism was described in breeding terns for which predation by gulls was temporarily impaired by human presence and associated research activities (Donehower et al. 2007; Riensche et al. 2012). In Dumont d'Urville, several colonies are situated under buildings (whose location may increase nest protection from skuas), but they were too few in number to include this dimension in our model. Moreover, no data exist at the scale of colonies on the number of skua predation attempts. Further data need to be collected to measure any local differences in predation pressures.

Local topography or micro-environment may be another important driver of Adélie penguins' colony breeding success (Acero and Aguirre 1994; Ainley 2002). Some colonies located directly under the buildings will be completely sheltered from the elements and avian predation (~2–3 colonies, Fig. 1). For exposed colonies, topographic variables selected in the model included aspect (i.e., slopes orientation of the colonies relative to geographic north) and windshelter index. These variables are related to the risk of snowdrift formation which is known to be an important driver affecting Adélie penguin breeding success (Fraser et al. 2013; Schmidt et al. 2021). Indeed, snowdrifts mainly form in areas protected from the dominant winds. Aspect gave a general indicator of the direction faced by colonies and windshelter index includes the wind protection induced by local topography. Although aspect did not seem to have any significant effect, breeding success decreased with windshelter index, probably due to higher snowdrift risk in wind-protected areas. Hence, snowdrift formation likely plays a role in breeding success, but its effect will likely depend on precipitations and wind storms whose occurrence and intensity vary annually. Still, the long duration of our study allowed us to capture the spatial variability in snowdrift risk induced by the topography. At the infrastructure scale, however, the spatial resolution of our model did not allow us to model the snowdrift formation risk induced by buildings. The infrastructures (buildings but also footbridges, tanks and other stationary equipment) generate multiple snowdrifts during the breeding season (Kwok et al. 1992). Depending on their position around the infrastructures, colonies can either be protected from the snowdrift risk or be subjected to it. How this artificial micro-environment contributes to colony breeding success remains unclear. The limited number of colonies within the core of the station compared to the rest of the study area makes statistical comparison of environmental characteristics challenging. Long-term analysis of local meteorological variables between areas of disturbance may help to characterize a potential micro-climate induced by the station. Still, the limited space available between the buildings seems to have

been colonized by penguins avoiding the main snowdrift areas and using all local humps (personal observations).

An indirect effect of the infrastructures that may affect breeding site selection around the station is the availability of excavated pebbles generated by road and building constructions. The precise granulometry of the pebbles used for nest construction—which are moved singly by penguins—is decisive in partner attraction (Ainley 2002). Adélie penguins developed a set of strategies to accumulate pebbles triggering inter-individual competition within and between colonies. Bigger nests reflect more intense individual effort to reproduce and are the most successful. They tend to be located at the center of the colonies where pebble removal pressure by conspecific is less intense (Morandini et al. 2021). Hence, areas saturated in pebbles of the adequate size could therefore reduce inter-individual competition and subsequent effort allocated to nest construction and maintenance. No systematic comparison has been conducted yet to compare the relative breeding success of nests between the center of the station and the rest of the study area.

Another behavioral selection in penguins may arise from a progressive habituation to human presence as suggested for Gentoo penguins (*Pygoscelis papua*) (Holmes et al. 2006) and other seabirds (Nisbet 2000). Habituation mechanisms may lower stress response (Bejder et al. 2009) and could therefore explain the maintained presence of breeding penguins within the station. Habituation, however, do not explain the higher breeding success of the colonies within the station. Personality traits may also have been selected in individuals nesting near humans with lower responses to stressful stimuli selecting bold personalities rather than shy ones (Cockrem 2007). Personality traits of individuals for which human presence is less impacting may be linked to a stronger motivation to reproduce with higher breeding success. Personality tests on the field in different disturbance areas coupled with stress response analysis will be instrumental to validate the hypothesis of penguins' personality selection through human presence or distance to facilities.

Projected maps of colony breeding success and colony growth rate are only poorly correlated. Indeed, the drivers of these population parameters diverged significantly. The main driver of colony growth rate was the topographical wetness index calculated downslope (TWID). We selected this index as a proxy of terrain drainage through topography. Indeed, the TWID calculates indices of terrain wetness based on the relative contribution of surrounding slopes. Accumulation of wetness in poorly drained areas may flood penguins' colonies with consequences on nests insulation from soil temperature and subsequent offspring survival. Interestingly, TWID increased both with colony breeding success and growth rate. We may explain this relationship, because higher TWID corresponds to flat areas located downslopes which are easily accessible by

penguins from the sea. At the beginning of the breeding season, these areas are mostly covered with snow and not yet submitted to flooding events. Moreover, this index is calculated at the resolution of the digital elevation model which does not integrate small eminences nor nest constructions used by penguins to isolate from running water and mud (Ainley 2002). Finally, zero TWID in our projections corresponds to areas not computed due to zero elevation in the digital elevation model. Therefore, the U-shape of the relationship between TWID and growth rate is probably artefactual, the topographical characteristics of zero TWID areas being more related to those of higher TWID areas. We therefore hypothesize that colony accessibility from the sea rather than potential wetness accumulation plays a role in initial colony formation and maintenance through time, especially considering that most of the breeding areas are uniformly covered with snow at the beginning of the reproductive cycle (personal observation).

According to the *public information hypothesis* (Danchin et al. 1998; Doligez et al. 2003), higher breeding success colonies are expected to attract new breeding pairs through prospecting of conspecific breeding success in the previous years. Interestingly, the annual growth rate of Adélie penguin colonies was highly correlated with a 1-year lag to colony breeding success, therefore supporting the hypothesis that prospecting new breeders may use public information to select their breeding site for the next year. Thus, colonies situated close to infrastructures experiencing higher breeding success may attract breeding individuals the following year, resulting in a positive association between colony growth rate and the proximity of infrastructures. In addition, colony size within the station is constrained by the surrounding infrastructures. Hence, the colonies within the core station area may be limited in their extension which may affect further density dependence mechanisms. However, experienced breeders are expected to recruit from the same colony every year (Ainley 2002), and therefore, competition for favorable colonies may mainly arise from unexperienced breeders during their first breeding attempts.

Our study revealed a strong spatial variability in Adélie penguin colonies breeding success and growth rate around the Dumont d'Urville research station. While predation seemed to be a relatively important driver of breeding success, human infrastructures were positively associated with an overall higher colonies breeding success. How these relationships impact the penguin population dynamics at the scale of the archipelago remains unclear. Demographic mechanisms at the colony scale should be investigated to assess potential source-sink mechanisms and how the proximity of infrastructures affect these dynamics. This would provide strong insights to decipher the contribution of

facility-related human disturbance on a long-lived Antarctic species population in a rapidly changing environment.

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**Author contribution statement** YM, KD, TR, CAB, and CB contributed to the study conception and design. Data curation was performed by YM and KD with support from JV, JA, and VD. Data analysis was performed by YM with input from KD, ASBL, TR, CAB, and CB. The manuscript was written by YM, and all authors contributed to the revisions and approved the final manuscript.

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**Data availability** Not applicable.

**Code availability** Data supporting the results are available from the Figshare Digital Repository: <http://doi.org/https://doi.org/10.6084/m9.figshare.22341229>.

## Declarations

**Conflict of interest** The authors declare no competing interests.

**Consent to participate** Not applicable.

**Consent for publication** Not applicable.

**Ethics approval** The Ethics Committee of IPEV and Comité de l'Environnement Polaire approved the field procedures.

## References

- Acerro JM, Aguirre CA (1994) A monitoring research plan for tourism in Antarctica. *Ann Tour Res* 21:295–302. [https://doi.org/10.1016/0160-7383\(94\)90046-9](https://doi.org/10.1016/0160-7383(94)90046-9)
- Ainley DG (2002) *The Adélie penguin: bellwether of climate change*. Columbia University Press, Columbia
- Ainley DG, DeMaster DP (1980) Survival and mortality in a population of adélie penguins. *Ecology* 61:522–530. <https://doi.org/10.2307/1937418>
- Barbraud C, Delord K, Weimerskirch H (2015) Extreme ecological response of a seabird community to unprecedented sea ice cover. *R Soc Open Sci* 2:140456. <https://doi.org/10.1098/rsos.140456>
- Barbraud C, Delord K, Bost CA et al (2020) Population trends of penguins in the French Southern Territories. *Polar Biol* 43:835–850. <https://doi.org/10.1007/s00300-020-02691-6>
- Bejder L, Samuels A, Whitehead H et al (2009) Impact assessment research: use and misuse of habituation, sensitisation and



- tolerance in describing wildlife responses to anthropogenic stimuli. *Mar Ecol Prog Ser* 395:177–185. <https://doi.org/10.3354/meps07979>
- Bergström L, Kautsky L, Malm T et al (2014) Effects of offshore wind farms on marine wildlife—a generalized impact assessment. *Environ Res Lett* 9:034012. <https://doi.org/10.1088/1748-9326/9/3/034012>
- Bivand R (2022) R packages for analyzing spatial data: a comparative case study with areal data. *Geogr Anal* 54(3):488–518. <https://doi.org/10.1111/gean.12319>
- Brenning A (2008) Statistical geocomputing combining R and SAGA: the example of landslide susceptibility analysis with generalized additive models. In: Böhner J, Blaschke T, Montanarella L (eds) SAGA - seconds out (Hamburger Beiträge zur Physischen Geographie und Landschaftsökologie, 19). pp 23–32. ISSN: 1866-170X
- Bricher PK, Lucieer A, Woehler EJ (2008) Population trends of Adélie penguin (*Pygoscelis adeliae*) breeding colonies: a spatial analysis of the effects of snow accumulation and human activities. *Polar Biol* 31:1397–1407. <https://doi.org/10.1007/s00300-008-0479-z>
- Burnham KP, Anderson DR, Anderson DR (2010) Model selection and multimodel inference: a practical information-theoretic approach, 2nd edn. Springer, New York
- Caccavo JA, Raclot T, Poupart T et al (2021) Anthropogenic activities are associated with shorter telomeres in chicks of Adélie penguin (*Pygoscelis adeliae*). *Polar Biol* 44:1391–1399. <https://doi.org/10.1007/s00300-021-02892-7>
- Carlini AR, Coria NR, Santos MM et al (2007) Breeding success and population trends in Adélie penguins in areas with low and high levels of human disturbance. *Polar Biol* 30:917–924. <https://doi.org/10.1007/s00300-006-0251-1>
- Cavaliere DJ, Parkinson CL (2012) Arctic sea ice variability and trends, 1979–2010. *Cryosphere* 6:881–889. <https://doi.org/10.5194/tc-6-881-2012>
- Ceballos G, Ehrlich PR, Barnosky AD et al (2015) Accelerated modern human-induced species losses: entering the sixth mass extinction. *Sci Adv* 1:1–5. <https://doi.org/10.1126/sciadv.1400253>
- Cimino MA, Lynch HJ, Saba VS, Oliver MJ (2016) Projected asymmetric response of Adélie penguins to Antarctic climate change. *Sci Rep* 6:1–9. <https://doi.org/10.1038/srep28785>
- Cockrem JF (2007) Stress, corticosterone responses and avian personalities. *J Ornithol* 148:169–178. <https://doi.org/10.1007/s10336-007-0175-8>
- Cockrem JF, Potter MA, Barrett DP, Candy EJ (2008) Corticosterone responses to capture and restraint in emperor and adélie penguins in Antarctica. *Zoolog Sci* 25:291–298. <https://doi.org/10.2108/zsj.25.291>
- Coetsee BWT, Chown SL (2016) A meta-analysis of human disturbance impacts on Antarctic wildlife: human disturbance impacts on Antarctic wildlife. *Biol Rev* 91:578–596. <https://doi.org/10.1111/brv.12184>
- Coetsee BWT, Convey P, Chown SL (2017) Expanding the protected area network in Antarctica is urgent and readily achievable: expanding Antarctica's protected areas. *Conserv Lett* 10:670–680. <https://doi.org/10.1111/conl.12342>
- Convey P, Peck LS (2019) Antarctic environmental change and biological responses. *Sci Adv* 5:1–16. <https://doi.org/10.1126/sciadv.aaz0888>
- Culik B, Adelung D, Woakes AJ (1990) The effect of disturbance on the heart rate and behaviour of Adélie penguins (*Pygoscelis adeliae*) during the breeding season. *Antarct Ecosyst*. [https://doi.org/10.1007/978-3-642-84074-6\\_18](https://doi.org/10.1007/978-3-642-84074-6_18)
- Danchin E, Boulinier T, Massot M (1998) Conspecific reproductive success and breeding habitat selection: implications for the study of coloniality. *Ecology* 79:2415–2428. [https://doi.org/10.1890/0012-9658\(1998\)079\[2415:CRSABH\]2.0.CO;2](https://doi.org/10.1890/0012-9658(1998)079[2415:CRSABH]2.0.CO;2)
- De Neve L, Fargallo J, Polo V et al (2006) Subcolony characteristics and breeding performance in the chinstrap penguin *Pygoscelis antarctica*. *Ardeola* 53:19–29
- Doligez B, Cadet C, Danchin E, Boulinier T (2003) When to use public information for breeding habitat selection? The role of environmental predictability and density dependence. *Anim Behav* 66:973–988. <https://doi.org/10.1006/anbe.2002.2270>
- Donehower CE, Bird DM, Hall CS, Kress SW (2007) Effects of gull predation and predator control on tern nesting success at Eastern Egg Rock, Maine. *Waterbirds Int J Waterbird Biol* 30:29–39
- Dorman M (2024) starsExtra: miscellaneous functions for working with 'stars' rasters. R package version 0.2.8. <https://github.com/michaeldorman/starsExtra/>, <https://michaeldorman.github.io/starsExtra/>
- Eayrs C, Li X, Raphael MN, Holland DM (2021) Rapid decline in Antarctic sea ice in recent years hints at future change. *Nat Geosci* 14:460–464. <https://doi.org/10.1038/s41561-021-00768-3>
- Emslie SD, Karnovsky N, Trivelpiece W (1995) Avian predation at penguin colonies on King George Island, Antarctica. *Wilson Bull* 107:317–327
- Erbe C, Marley SA, Schoeman RP et al (2019) The effects of ship noise on marine mammals—a review. *Front Mar Sci* 6:1–41. <https://doi.org/10.3389/fmars.2019.00606>
- Fraser W, Patterson-Fraser D, Ribic C et al (2013) A nonmarine source of variability in Adélie penguin demography. *Oceanography* 26:207–209. <https://doi.org/10.5670/oceanog.2013.64>
- Gaw S, Thomas KV, Hutchinson TH (2014) Sources, impacts and trends of pharmaceuticals in the marine and coastal environment. *Philos Trans R Soc B Biol Sci* 369:1–11. <https://doi.org/10.1098/rstb.2013.0572>
- Giese M (1996) Effects of human activity on adélie penguin *Pygoscelis adeliae* breeding success. *Biol Conserv* 75:157–164. [https://doi.org/10.1016/0006-3207\(95\)00060-7](https://doi.org/10.1016/0006-3207(95)00060-7)
- Gutt J, Isla E, Xavier JC et al (2021) Antarctic ecosystems in transition—life between stresses and opportunities. *Biol Rev* 96:798–821. <https://doi.org/10.1111/brv.12679>
- Holmes ND, Giese M, Achurch H et al (2006) Behaviour and breeding success of gentoo penguins *Pygoscelis papua* in areas of low and high human activity. *Polar Biol* 29:399–412. <https://doi.org/10.1007/s00300-005-0070-9>
- Horváth Z, Ptacnik R, Vad CF, Chase JM (2019) Habitat loss over six decades accelerates regional and local biodiversity loss via changing landscape connectance. *Ecol Lett* 22:1019–1027. <https://doi.org/10.1111/ele.13260>
- Howat IM, Porter C, Smith BE et al (2019) The reference elevation model of Antarctica. *Cryosphere* 13:665–674. <https://doi.org/10.5194/tc-13-665-2019>
- König-Langlo G, King JC, Pettré P (1998) Climatology of the three coastal Antarctic stations Dumont d'Urville, Neumayer, and Halley. *J Geophys Res Atmospheres* 103:10935–10946. <https://doi.org/10.1029/97JD00527>
- Kwok KCS, Kim DH, Smedley DJ, Rohde HF (1992) Snowdrift around buildings for Antarctic environment. *J Wind Eng Ind Aerodyn* 44:2797–2808. [https://doi.org/10.1016/0167-6105\(92\)90073-J](https://doi.org/10.1016/0167-6105(92)90073-J)
- Lee JR, Raymond B, Bracegirdle TJ et al (2017a) Climate change drives expansion of Antarctic ice-free habitat. *Nature* 547:49–54. <https://doi.org/10.1038/nature22996>
- Lee S, Volkov DL, Lopez H et al (2017b) Wind-driven ocean dynamics impact on the contrasting sea-ice trends around West Antarctica. *J Geophys Res Oceans* 122:4413–4430. <https://doi.org/10.1002/2016JC012416>
- Marra G, Wood SN (2011) Practical variable selection for generalized additive models. *Comput Stat Data Anal* 55:2372–2387. <https://doi.org/10.1016/j.csda.2011.02.004>

- McCarthy AH, Peck LS, Hughes KA, Aldridge DC (2019) Antarctica: the final frontier for marine biological invasions. *Glob Change Biol* 25:2221–2241. <https://doi.org/10.1111/gcb.14600>
- Micol T, Jouventin P (2001) Long-term population trends in seven Antarctic seabirds at Pointe Géologie (Terre Adélie). *Polar Biol* 24:175–185
- Morandini V, Dugger KM, Lescroël A et al (2021) Maintenance of nest quality in Adélie penguins *Pygoscelis adeliae*: an additional benefit to life in the center. *Polar Biol* 44:1553–1562. <https://doi.org/10.1007/s00300-021-02894-5>
- Moret GJM, Huerta AD (2007) Correcting GIS-based slope aspect calculations for the Polar Regions. *Antarct Sci* 19:129–130. <https://doi.org/10.1017/S0954102007000181>
- Naimi B, Hamm Na, Groen TA, Skidmore AK, Toxopeus AG (2014) Where is positional uncertainty a problem for species distribution modelling. *Ecography* 37:191–203. <https://doi.org/10.1111/j.1600-0587.2013.00205.x>
- Nisbet IT (2000) Disturbance, habituation, and management of waterbird colonies. *Waterbirds* 2:312–332
- Pacoureau N, Authier M, Delord K, Barbraud C (2019a) Population response of an apex Antarctic consumer to its prey and climate fluctuations. *Oecologia* 189:279–291. <https://doi.org/10.1007/s00442-018-4249-5>
- Pacoureau N, Delord K, Jenouvrier S, Barbraud C (2019b) Demographic and population responses of an apex predator to climate and its prey: a long-term study of South Polar Skuas. *Ecol Monogr* 89:1–15. <https://doi.org/10.1002/ecm.1388>
- Pebesma E (2018) Simple Features for R: Standardized Support for Spatial Vector Data. *R J* 10(1):439–446. <https://doi.org/10.32614/RJ-2018-009>
- Pebesma E (2024) lwgeom: Bindings to Selected 'liblwgeom' functions for simple features. R package version 0.2-14. <https://github.com/r-spatial/lwgeom>, <https://r-spatial.github.io/lwgeom/>
- Pertierra LR, Hughes KA, Vega GC, Olalla-Tárraga MÁ (2017) High resolution spatial mapping of human footprint across Antarctica and its implications for the strategic conservation of avifauna. *PLoS ONE* 12:1–20. <https://doi.org/10.1371/journal.pone.0168280>
- Polar Geospatial Center, University of Minnesota Reference Elevation Model of Antarctica. <https://data.pgc.umn.edu/elev/dem/setsm/REMA>
- Post E, Alley RB, Christensen TR et al (2019) The polar regions in a 2°C warmer world. *Sci Adv* 5:eaaw9883. <https://doi.org/10.1126/sciadv.aaw9883>
- Purich A, Cai W, England MH, Cowan T (2016) Evidence for link between modelled trends in Antarctic sea ice and underestimated westerly wind changes. *Nat Commun* 7:1–9. <https://doi.org/10.1038/ncomms10409>
- QGIS.org (2019) QGIS geographic information system. QGIS Association. <http://www.qgis.org>
- R Core Team (2023) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>
- Riensch DL, Kitting CL, Groff TC et al (2012) California gull predator management and reproductive success of endangered California least terns in the San Francisco Bay, California. *Proc Vertebr Pest Conf*. <https://doi.org/10.5070/V425110504>
- Ropert-Coudert Y, Kato A, Meyer X et al (2015) A complete breeding failure in an Adélie penguin colony correlates with unusual and extreme environmental events. *Ecography* 38:111–113. <https://doi.org/10.1111/ecog.01182>
- Ropert-Coudert Y, Kato A, Shiomi K et al (2018) Two recent massive breeding failures in an adélie penguin colony call for the creation of a marine protected area in D'Urville Sea/Mertz. *Front Mar Sci* 5:264. <https://doi.org/10.3389/fmars.2018.00264>
- Roy P, Mohanty AK, Misra M (2022) Microplastics in ecosystems: their implications and mitigation pathways. *Environ Sci Adv* 1:9–29. <https://doi.org/10.1039/D1VA00012H>
- Schmidt AE, Ballard G, Lescroël A et al (2021) The influence of subcolony-scale nesting habitat on the reproductive success of Adélie penguins. *Sci Rep* 11:1–15. <https://doi.org/10.1038/s41598-021-94861-7>
- Taylor RH (2008) The Adélie penguin *pygoscelis adeliae* at Cape Royd. *Ibis* 104:176–204. <https://doi.org/10.1111/j.1474-919X.1962.tb08644.x>
- Waters CN, Zalasiewicz J, Summerhayes C et al (2016) The anthropocene is functionally and stratigraphically distinct from the Holocene. *Science* 351:1–10. <https://doi.org/10.1126/science.aad2622>
- Wilson DJ, Lyver PO, Greene TC et al (2017) South Polar Skua breeding populations in the Ross Sea assessed from demonstrated relationship with Adélie penguin numbers. *Polar Biol* 40:577–592. <https://doi.org/10.1007/s00300-016-1980-4>
- Winstral A, Elder K, Davis RE (2002) Spatial snow modeling of wind-redistributed snow using terrain-based parameters. *J Hydrometeorol* 3:524–538. [https://doi.org/10.1175/1525-7541\(2002\)003%3c0524:SSMOWR%3e2.0.CO;2](https://doi.org/10.1175/1525-7541(2002)003%3c0524:SSMOWR%3e2.0.CO;2)
- Woehler EJ, Penney RL, Creet SM, Burton HR (1994) Impacts of human visitors on breeding success and long-term population trends in Adélie penguins at Casey, Antarctica. *Polar Biol* 14:269–274. <https://doi.org/10.1007/BF00239175>
- Wood S (2017) Generalized additive models: an introduction with R, 2nd edn. Chapman and Hall/CRC. <https://doi.org/10.1201/9781315370279>
- Wu Q, Brown A (2022) 'whitebox': 'WhiteboxTools' R Frontend. R package version 2.2.0. <https://CRAN.R-project.org/package=whitebox>

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