

Article

Breeding Ecology of Adélie Penguins in Mid Victoria Land, Ross Sea Antarctica

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Abstract: Identifying the factors influencing seabird breeding output is critical for their conservation because breeding performance in turn influences population dynamics. This is particularly important in sensitive environments, where ecological disturbances can lead to changes in population trends of extremely specialized species in a relatively short time. Here, we have reported on the breeding output of the Adélie penguin *Pygoscelis adeliae* in three colonies of the Mid Victoria Land, Ross Sea (Antarctica), in 2017/2018–2018/2019 to provide scientific information for the Ross Sea Marine Protected Area research and management plan. Breeding chronology, breeding success and chick growth did not differ between study colonies and were in line with data reported for other penguin colonies across Antarctica. Penguin breeding success was higher in central than in peripheral nests and decreased with an increasing number of neighboring nesting skuas; conversely, at-nest weather conditions experienced by chicks did not seem to play a role. Our findings suggest that the quality of the nesting environment seems more important than the general condition of the colony in determining breeding output. Therefore, along with marine habitat characteristics for the planning of management and conservation of seabirds, the importance of the terrestrial environment must be also duly considered.

Keywords: Adélie penguin; Antarctic species; breeding ecology; hatching success; breeding success; colony habitat; marine protected area; nest quality; seabirds; skua



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1. Introduction

The breeding ecology of seabirds can be used as an indicator of changes in lower trophic levels [1–3]. The variability in reproductive success and timing of seabirds reflects the variability in food resources, which in turn depends on complex ocean/atmosphere interactions [4,5]. Environmental factors differ among locations and among years, affecting the accessibility and availability of food resources and ultimately the reproductive success of marine birds [6–8]. Identifying the factors that influence seabird breeding output is critical for their conservation because breeding performance in turn influences population dynamics. This is particularly important in sensitive environments such as Antarctica, where ecological disturbances can lead to changes in population trends of extremely specialized species in a relatively short time [9,10].

Marine predators, like Antarctic seabirds, have been recognized as key species in the identification, design, implementation, and monitoring of Marine Protected Areas (MPAs) [11–13]. MPAs provide protection at both breeding sites and foraging areas for seabirds. Moreover, at a larger scale, MPAs can maintain connectivity between breeding and non-breeding sites and can guarantee the protection of potentially suitable refuge

areas [10]. The Ross Sea region MPA came into force in December 2017. It covers 1.55 million km² of ocean and protects a unique ecosystem and its marine species, biodiversity, and habitats [14,15]. The associated Research and Monitoring Plan [16] requires multidisciplinary research on key species as indicated in the CCAMLR Conservation Measure Annex 91-05/C [17]. During 2017–2019, the Italian project PenguinERA investigated the ecological role of a marine predator, the Adélie penguin *Pygoscelis adeliae*, through the study of its distribution and behavior in relation to the quality of habitat, colony size, evolution, and adaptation at the scales of the ecological and climatic processes [18]. The study area involved three Adélie penguin colonies located between Terra Nova Bay and Wood Bay (Ross Sea, Antarctica). The existing long-term monitoring program was improved by measuring a series of different bioecological parameters to contribute to the Ross Sea MPA Research and Monitoring Plan [19].

Because of the high degree of connectivity between sea and land and as part of the larger project, we evaluated the factors that may influence breeding output and performance in the Adélie penguin. The reproduction of the Adélie penguin is a highly synchronized event that takes place during the short Antarctic summer. The Adélie penguin breeding season runs from October to February; it can be slightly shorter or longer depending on the latitude at which the colony is located and on local environmental conditions [20,21]. Amongst the physical factors that may influence the reproductive success of this species, sea ice plays a critical role [22]. A delay in the summer breakup of the sea ice can reduce the reproductive success of Adélie penguins because of the influence that ice has on the abundance and distribution of prey species [23,24]. Moreover, extensive sea ice makes it energetically more expensive to travel between the colony and feeding areas [25]. In winter, the ice extent can also increase the mortality of juvenile individuals, resulting in a reduced number of occupants of these colonies several years after the event [26,27]. However, the effects of sea ice on the reproductive biology of the Adélie penguin are twofold. In the western area of the Antarctic Peninsula, the gradual decrease in sea ice cover was a limiting factor [28,29]. Although the effects of environmental factors such as sea ice extent/concentration and sea temperature on breeding output have been largely investigated for strictly Antarctic seabirds [30,31], the effects of the terrestrial environment have been under-studied. Factors related to the quality of the nesting habitat, especially the proximity and number of terrestrial predators, the location of the nesting environment and weather conditions experienced at the nest have been often overlooked, with a few exceptions [32–34]. Yet, predator–prey relationships and harsh weather can strongly influence breeding output and population dynamics as much as other factors like food availability [35–38].

Adélie penguin colonies in the Mid Victoria Land are relatively close to each other but exposed to different local sea ice conditions and differ as much as tenfold in breeding population size [39–41]. Intraspecific competition over food resources may have cascading effects on foraging strategies, diet, and breeding performance of penguins [37], and the presence of the Terra Nova Bay polynya may play an important role in facilitating access to foraging areas, reducing the energy–time budget for breeders throughout the reproductive season [25,39]. Breeding success, in the long-term, contributes to colony size [42] and the quality of the terrestrial habitat can thus be an important driver of population growth [34]. The aims of our study were: (1) to report the breeding output of the Adélie penguin in three neighboring colonies inhabited by the metapopulation of Mid Victoria Land; (2) to identify factors of the terrestrial environment possibly affecting hatching and breeding success in this seabird by focusing on two colonies monitored regularly at the fine scale and (3) to provide scientific information on an indicator species, i.e., the Adélie penguin, for the Ross Sea MPA research and management plan [16].

2. Materials and Methods

2.1. Study Areas and Ecological Background

Our study took place for two summer seasons, November to February 2017–2018 and 2018–2019. The Adélie penguin population was monitored to compare breeding chronology and success among colonies located between Wood Bay and Terra Nova Bay on a 75 km stretch of coast along central Victoria Land, Ross Sea, Antarctica (Figure 1). The ecological features of the three penguin colonies (Inexpressible Island, InIs, 74°54' S, 163°39' E; Adélie Cove, AdCo, 74°46' S, 164°00' E; Edmonson Point, EdPo, 74°20' S, 165°08' E), i.e., marine and colony habitats that characterize these sites, have been detailed in a previous study [40]. Colony size was markedly greater at InIs than at AdCo and EdPo, with the latter showing the lowest population size. EdPo has the lowest habitat quality, with the highest per capita density of terrestrial predators (South Polar skua *Stercorarius maccormicki*), the farthest distance from polynya and the greatest extension of fast ice. The main differences in penguin population abundance, seasonal sea ice regimes, and density of terrestrial predators occurring among the study colonies are summarized in Table 1.

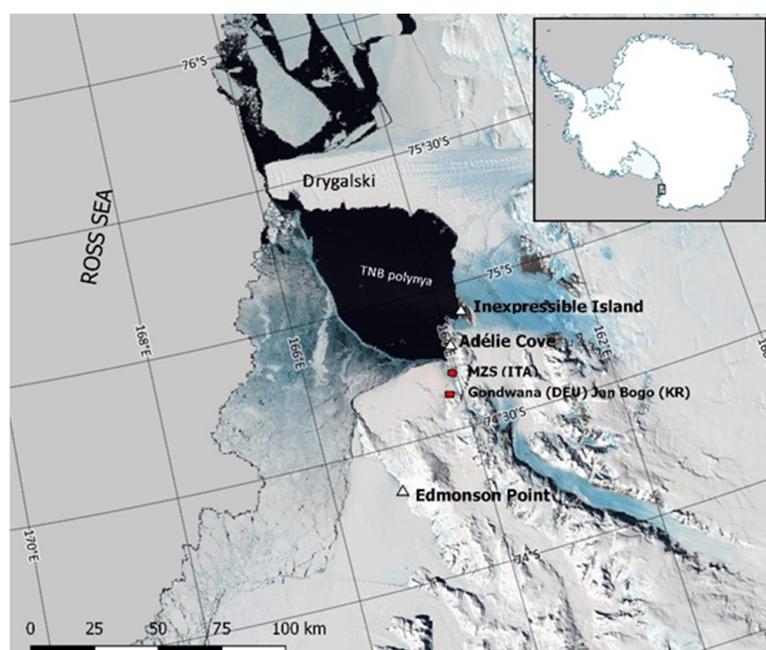


Figure 1. Map of the three study areas located in the Ross Sea (modified by [40]).

Table 1. Ecological features of the three colonies located in central Victoria Land, Ross Sea, Antarctica. The linear distance to Terra Nova Bay polynya and range of fast ice extension was measured using EOSDIS Worldview [42] to the best image available in late October, mid-December, and mid-January from 2017 to 2019. The approximate size of the colony area was measured with Google Earth Pro on images on the 23 February 2010, 27 November 2011 and 2 December 2011 for Edmonson Point, Adélie Cove, and Inexpressible Island, respectively, updated from [40].

	N. of Nests	Colony Area (km ²)	Skua Nests ^c	Linear Fast Ice Extension (max–min, km)	Linear Distance to Polynya (km)
EdPo	2704 ^a	0.03	105; 78	36–13; 32–13	44
AdCo	11,438 ^b	0.06	25; 30	5–0; 2–0	0
InIs	29,899 ^b	0.25	29; 35	3.5–0; 0.5–0	0

^a Data from ground census of 29 November 2017, this study. ^b Data from aerial census of 2018 and 2019 [43].

^c Data from ground census (December 2017 and 2018, this study).

The annual life cycle of Adélie penguins is characterized by a short and highly synchronized breeding period (Figure 2). Penguins arrive at the breeding colonies from mid-October, with males arriving a few days earlier than females. Both parents share the task of incubating the eggs, alternating at the nest during the 32–34 days necessary for hatching. The chicks remain at the nest and are fed and protected up to about 22 days of age (guard phase). In the following period (crèche phase), chicks tend to leave the nest and gather in groups with chicks from nearby nests, returning to the nest area only to receive a meal from their parents. During this period the diet varies between locations, breeding stages, and supply areas. It consists of variable amounts of krill (*Euphausia superba* and *E. crystallophias*) and fish (*Pleuragramma antarcticum* and juvenile stages of *Notothenioidei*) [44]. Chicks leave the colony by the end of February at the age of 50–60 days (fledge phase). Parents and non-breeding adults may remain to molt at breeding colonies or leave earlier to molt at sea. Young Adélie penguins first return to their natal colony at 2–4 years of age, but rarely they attempt to breed on the first visit [44].

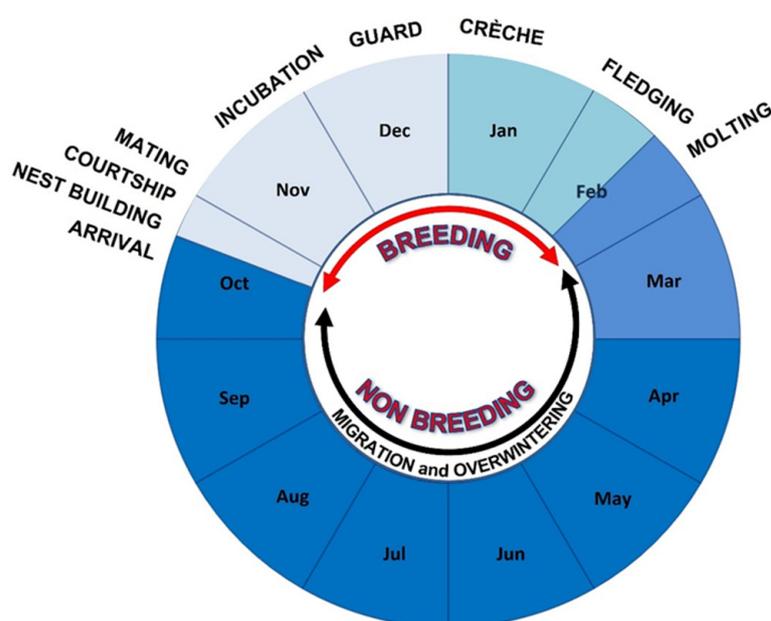


Figure 2. Adélie penguin annual cycle.

2.2. Naïve Estimation of Breeding Success (Three Colonies-Comparison)

Breeding output was compared among the three colonies by counting visually the number of nests with eggs and the number of chicks per nest over large sectors [45,46]. At EdCo, standardized counts have been conducted since 1994, according to the well-established CCAMLR Ecosystem Monitoring Program methodology [45,46]. The colony area and population abundance at AdCo and InIs were too large to allow a ground count over a large area. Thus, for both colonies, we selected three distinct subcolonies of about 70–100 nests each, at a distance of at least 100 m from one another (for a total of 210–300 nests per colony) and counted the number of nests with eggs and the number of chicks within each of them.

In all colonies, the number of nests with eggs was counted in the period 28 November–6 December when peak laying has occurred and usually only one parent occupies the nest [47]. In the same groups, the total number of chicks per nest was counted in mid-January, when usually 2/3 of chicks have entered the crèche stage. A naïve estimation of breeding success at each colony was calculated as the number of chicks counted divided by the number of nests with eggs [32,34].

2.3. Hatching and Breeding Success (Two Colonies-Comparison)

At Edmonson Point, long-term data on breeding output for individual nests have been collected in previous seasons [46]. The vicinity of Adélie Cove colony to MZS allowed

us to include more detailed data in the two seasons also for this colony. For both study years, at the beginning of the breeding season (early November), 40–70 occupied nests per colony were selected and marked with plastic tags fixed in the ground (Figure 3). Adélie penguin colonies are composed of numerous separated subgroups of different sizes and shapes [44]; therefore, we attempted to balance sampling spatially. We selected both peripheral and central nests [48] in different subgroups within each colony to investigate potential differences related to nest characteristics (e.g., predation risk). However, as our study was carried out throughout the breeding period, no central nest located beyond three nests from the colony edge was sampled to limit disturbance to the other breeders. Nests were visited and monitored every 1–3 days at Edmonson Point and every 5–7 days at Adélie Cove. From hatching until the end of brooding, observations of the marked nests were carried out, and the identity of the bird was recorded together with the number of chicks and eggs. Where necessary, a handheld tag reader was used to identify adult birds previously marked with passive transponders tags (TIRIS™ Texas Instruments Registration and Identification System) at their nests. Capturing and handling of adults and chicks were carried out according to the SCAR code of conduct, as reported in previous studies [39].



Figure 3. Monitoring of penguin and skua nests: (a) an Adélie penguin nest marked at Adélie Cove and (b) a skua nesting around subcolonies marked with GPS at Edmonson Point (photo silviaolmastroni@PNRA2017).

2.4. Chick Growth (Two Colonies-Comparison)

During the seasons 2017/2018 and 2018/2019, chicks at marked nests were monitored and weighted regularly (i.e., 5–8 days) with Pesola spring scales. Hatching dates and weight were recorded to compare the chick growth rate between colonies. During 2017/2018, harsh weather made it difficult to visit AdCo on a regular basis in the second part of the season; therefore, the chick growth curve for 2017/2018 is available for EdPo only.

2.5. Predation Risk (Two Colonies-Comparison)

To investigate the influence of predation risk by skua on penguin hatching and breeding success, we mapped all skua nests in our study colonies, in both years, using a portable GPS (Figure 3). It has been shown that breeding skua pairs can travel 50–80 m from their nests into a penguin colony while looking for eggs and chicks [49]; moreover, the median size of skua feeding territory is about 1.1 ha [50], which would correspond to circular territories of about a 60 m radius. Accordingly, Schmidt et al. [34] considered the presence of skua nests within 50 m of the penguin colony edge to investigate the effect of skua predation pressure on penguin breeding success. Earlier research conducted at EdPo has also shown that skua pairs nesting within 50 m from penguin nests, especially skuas nesting within 15 m, have a higher fledging success [51], suggesting that distances closer than

50 m from penguin nests can facilitate predation on penguins by skuas. Following the above studies, we thus considered the number of skua pairs within distances of 50 m and 100 m around penguin nests. We used Quantum Gis 2.18.23 (Quantum Gis Development Team 2015) to calculate the number of skua nests surrounding each penguin nest, by the following steps: (i) we drew circular buffers of 50 m and 100 m radii around each penguin nest; (ii) we overlapped and intersected them with the distribution map of skua nests; (iii) we calculated the number of skua nests within circular buffers.

2.6. At Nest-Weather (Two Colonies-Comparison)

Weather at the two colonies was determined from data of the weather stations ‘K3’ and ‘Rita’ for AdCo (‘Rita’ was used only in 2018/2019, starting from 29 December onwards, due to malfunctioning of ‘K3’) and ‘Penguin’ for EdPo (data from ENEA Antarctica Technical Unit for Logistics Service for K3 and the PNRA Antarctic Meteo-Climatological Observatory). Meteorological data recorded every 10 min at weather stations were averaged daily in order to calculate mean daily weather parameters [39]. We used the period 20 November–20 January (62 days), i.e., the period when data were available for both colonies and years, to formally test the weather differences between the two colonies in each study year. Differences in mean daily weather parameters between colonies were tested through the nonparametric paired sign test to account for repeated measurements in the two colonies conducted on the same day, which allowed to control for the effect of the day on weather [39]. Weather was generally harsher at AdCo, with slightly lower temperatures and windchill than at EdPo in both study years, and greater wind speed and relative humidity in the first study year (Table 2).

Table 2. Differences in mean daily measurements (\pm standard error) of weather parameters between colonies, for both study years. Weather parameters were averaged over 62 days (20 November–20 January) and differences were tested through the paired sign test (the test statistic, r , is reported). An asterisk marks significant ($p < 0.05$) comparisons.

	2017/2018			2018/2019		
	AdCo	EdPo	Test Statistic	AdCo	EdPo	Test Statistic
Wind speed (knots)	9.36 \pm 0.75	4.12 \pm 0.20	$r = 58$ ($p < 0.001$) *	6.01 \pm 0.41	6.36 \pm 0.54	$r = 39$ ($p = 0.055$)
Temperature ($^{\circ}$ C)	−4.98 \pm 0.22	−3.11 \pm 0.25	$r = 55$ ($p < 0.001$) *	−4.21 \pm 0.24	−1.96 \pm 0.27	$r = 58$ ($p < 0.001$) *
Windchill ($^{\circ}$ C)	−12.35 \pm 0.37	−8.57 \pm 0.24	$r = 59$ ($p < 0.001$) *	−12.42 \pm 0.41	−8.17 \pm 0.23	$r = 59$ ($p < 0.001$) *
Relative humidity (%)	62.37 \pm 1.57	56.83 \pm 1.72	$r = 40$ ($p = 0.030$) *	62.17 \pm 1.74	61.18 \pm 2.10	$r = 37$ ($p = 0.162$)

Severe weather conditions experienced at the nest may influence penguin breeding ecology in different ways. For example, weather-dependent heat loss by chicks could be expected to detrimentally affect the store of fat reserves by increasing their energetic demands for thermoregulation, reducing body growth and thus the probability to enter the crèche. To investigate meteorological effects, we considered the windchill as a comprehensive metric of weather harshness incorporating the effects of air temperature, air humidity and wind speed. Indeed, such a metric has been shown to affect Adélie penguin breeding success [32]. We followed the formulas provided by Smiley and Emmerson [32] to calculate the mean daily windchill in our study colonies and years. Because we expected the effect of weather to impact the chicks’ energetic trade-off, we considered the nest-specific mean daily windchill experienced by penguin chicks from the hatching date to the last census as a covariate for modeling breeding success (see below).

2.7. Breeding Chronology (Two Colonies-Comparison)

The deployment of two automated time-lapse cameras (Figure 4) aimed at recording penguin breeding phenology, also integrating data from field observations. A Penguin

Nest Camera (PNC49) was installed at EdPo in December 2014 in collaboration with the Australian Antarctic Division [52] as part of an international monitoring network [53]. A time-lapse imaging system, model Cyclapse Harbotronics was installed at AdCo at the end of the 2017/2018 season. The camera was provided by the ENEA Antarctica Technical Unit for Logistics Service and took a picture each 4 h during the breeding season. These instruments monitored an area including approximately 30 control nests. Observation made from available images recorded during the two breeding seasons helped in documenting phenology events at both colonies from October to February (first arrival, hatching, cr ching, fledging). For details on working periods of remotely-operated cameras, see Supplementary Material.

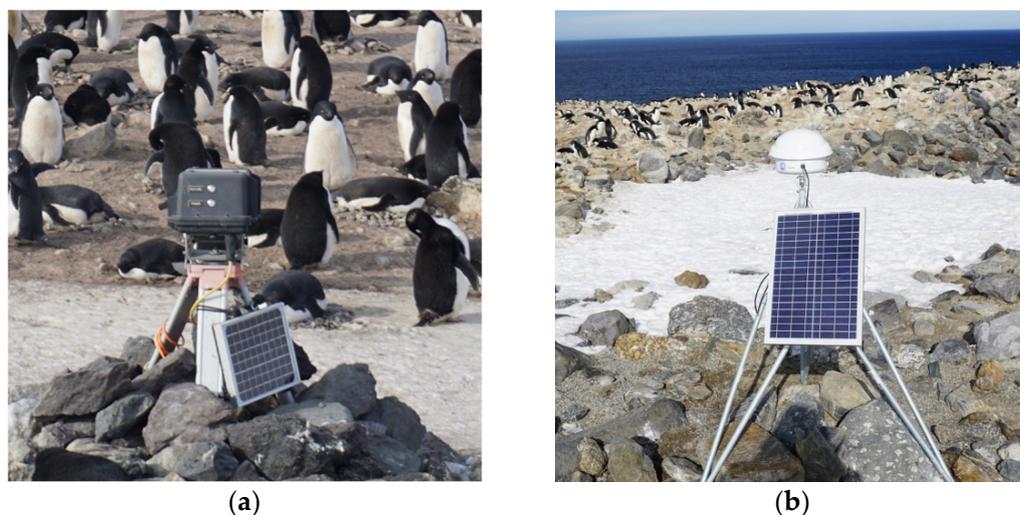


Figure 4. Remotely operated time-lapse cameras: (a) the Penguin Nest Camera at Edmonson Point, (b) Cyclapse Harbotronics at Ad lie Cove (photo silviaolmastroni@PNRA2017).

2.8. Statistical Analyses (Two Colonies-Comparison)

We evaluated two metrics of breeding output at the nest level: hatching success (the number of eggs hatched over the number of eggs laid) and breeding success (the number of chicks successfully cr ched over the number of eggs laid). Both indices are commonly used to quantify the effects of ecological and life-history variables on the breeding performance of colonial seabirds and have been implemented routinely on the Ad lie penguin [32,46]. As for hatching success, we considered for analysis all the nests monitored from incubation through the cr che stage ($N = 150$ nests; $N = 224$ data points). For breeding success, we retained nests where at least one egg hatched ($N = 143$ nests; $N = 199$ data points) because a mean hatching date per nest was needed to control for the decreasing probability of a chick's survival after the hatching date. Indices of breeding output were analyzed through generalized linear models (GLMs) using binomial errors and a logit link by setting the ratio between successes and trials as the response variable and considering the number of trials as the weight [54]. For both hatching and breeding success, we included five predictors: (1) colony (reference level: AdCo); (2) nest position (reference level: central nests); (3) year (reference level: summer 2017/2018); (4) number of skua nests within a circular buffer of 50 m around the focal penguin nest (integer, range: 0 to 8 nests, median: 2); (5) number of skua nests within a circular buffer of 100 m around the focal penguin nest (integer, range: 2 to 21 nests, median: 9). For breeding success, we also added as predictors: (6) the mean windchill experienced by focal nest's chicks between the hatching date and the last observation (continuous, range: -12.7 to -7.1 $^{\circ}\text{C}$, median: -7.9); (7) the number of days elapsed from hatching date to the last observation of the focal nest's chicks (integer, range: 7 to 32 days, median: 21). Data exploration confirmed the absence of nonlinear effects and no multicollinearity amongst covariates ($|r| < 0.5$). Covariates were scaled to allow the comparison of effect sizes.

For each response variable, we conducted a model selection according to the information-theoretic approach [55]. Each model evaluated had a different combination of predictors, and thus represented a different plausible hypothesis. The null model was also included for comparison with candidate models [56]. Candidate models were ranked and weighted. For model selection, we considered the AICc value of each model (i.e., the Akaike Information Criterion corrected for small sample size) and its difference with respect to the model with the lowest AICc value, i.e., ΔAICc . Following the “nesting rule” [55,57], we did not select models with $\Delta\text{AICc} \geq 2$ with respect to the best model (the model with the lowest AICc value), as well as models with an AICc value greater than that of any simpler alternative. Therefore, we obtained either a set of top-ranked models or a single best model for each response variable. The Akaike model weight was standardized within the subset of selected models and inference about the effects of predictors was made using the best model. For each response variable, we estimated coefficients of predictors and 95% confidence intervals from the best model.

As for chick growth, we fitted a linear mixed model (LMM) to compare chick mass between EdPo and AdCo over five time periods during the chick-rearing phase in the year 2018/2019. These time periods were established arbitrarily between the hatching date and when chicks entered the crèche [39]: 0–5 days from the hatching date, 6–10 days, 11–15 days, 16–20 days, 21–27 days. We included the colony as a categorical predictor (reference level: AdCo), and time period and nest identity as crossed random intercepts to account for repeated measurements in the same period and on the same nest. The response variable, i.e., chick mass, was ln-transformed to improve model residuals.

For all models, the effects of predictors were assessed by checking whether 95% confidence intervals of coefficients overlapped 0. All models were validated by visual inspection of residual patterns [54]. We conducted model selection, GLMs and the LMM through the R packages MuMIn [58], glmmTMB [59] and lme4 [60], respectively.

3. Results

Our naïve estimation of breeding success reported similar mean values among the three colonies (0.97–1.05 chicks raised to crèche per nest with eggs; Figure 5). Reproductive success was generally lower at EdPo and AdCo in 2017/2018 than 2018/2019 (Figure 5).

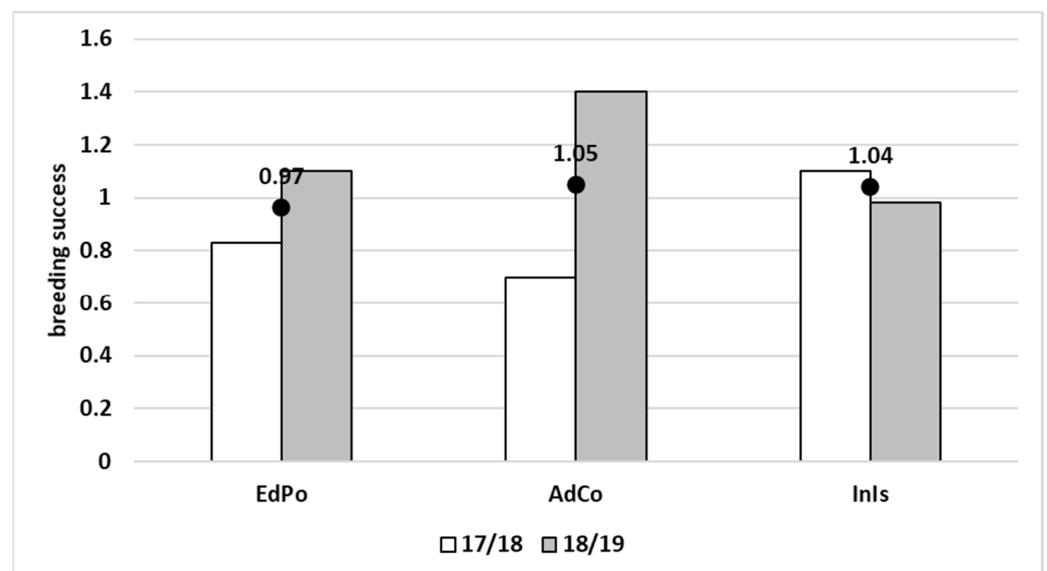


Figure 5. Breeding success for the three colonies in 2017/2018 (white bars) and 2018/2019 (gray bars). Black dot is the mean value across the two study years. Data for InIs in 2018/2019 were retrieved from [43].

3.1. Breeding Chronology in the Two Colonies

Images from remotely operated time-lapse cameras showed that the first arrival at Edmonson Point was recorded on 18 October 2017 and 19 October 2018 (data for Adélie Cove were not available). Chicks started entering the crèche from 5 January and 2 January at EdPo and 2 January and 31 December at AdCo in 2017/2018 and 2018/2019 respectively. In total, 2/3 of chicks were crèched by 10 January 2018 and 9 January 2019 for EdPo, and 10 January 2018 and 6 January 2019 at AdCo. On 16 February 2018 for EdPo and 15 February 2018 and 18^t February 2019 for AdCo, the control areas monitored by time-lapse cameras were completely void of penguins, indicating that juveniles and adults moved to beaches and to sea to fledge and start their migration.

Analyses of data obtained through nest monitoring for AdCo and EdPo showed that hatching occurred slightly earlier at AdCo than at EdPo in both years (median date; 2017/2018: AdCo, 14 December; EdPo, 16 December; 2018/2019: AdCo, 13 December; EdPo, 14 December).

3.2. Factors Influencing Hatching and Breeding Success in the Two Colonies

Only one model was selected to explain hatching success ($k = 3$, $AICc = 345.5$, $\Delta AICc = 0$, weight = 1) supporting the effects of nest position and study year on the probability of hatching. In particular, hatching success decreased by ~14% in peripheral nests and was ~17% greater in 2018/2019 (Table 3; Figure 6). As to breeding success, two models were selected, each with a similar probability of being the best model. The best model ($k = 5$, $AICc = 413.6$, $\Delta AICc = 0$, weight = 0.501) supported the effects of nest position, the number of skua nests surrounding the penguin nests and days elapsed from hatching date on breeding success. The estimated confidence intervals of the effect of windchill experienced by chicks in the early life stage overlapped '0' (Table 3). The effect of this variable was not supported by the second-best model ($k = 4$, $AICc = 413.6$, $\Delta AICc = 0.01$, weight = 0.499), which was the only difference with the top-ranking model. Breeding success decreased with days elapsed from hatching date. Accounting for such a confounding effect, the probability of a chick entering the crèche successfully decreased with the increasing number of skua nests in the surrounding 50 meters (Table 3, Figure 7a) and was predicted to be ~15% lower for peripheral than for central nests (Table 3, Figure 7b). The effect of predation risk was the greatest amongst predictors, so penguin nests with no skua nests within 50 m were predicted to show a ~60% greater breeding success than those surrounded by 8 skuas within 50 m (i.e., the maximum observed).

Table 3. Parameters estimated from top-ranked GLMs predicting hatching and breeding success in Adélie penguin: coefficients (β) and their 95% CIs. Reference levels for nest position and year are central nests and 2017/2018, respectively. An asterisk marks coefficients whose CIs do not include '0'.

Breeding Output Index	Predictor	β Coefficient	95% CI
Hatching success	Intercept	1.659	1.102; 2.216 *
	Nest position (peripheral)	-0.931	-1.533; -0.328 *
	Year (2018/2019)	0.766	0.274; 1.259 *
Breeding success	Intercept	0.776	0.381; 1.171 *
	Skuas' nests in 50 m	-0.523	-0.767; -0.278 *
	Nest position (peripheral)	-0.494	-0.961; -0.027 *
	Days elapsed from hatching date	-0.230	-0.444; -0.016 *
	Mean daily windchill (°C) from hatching date	0.181	-0.063; 0.426

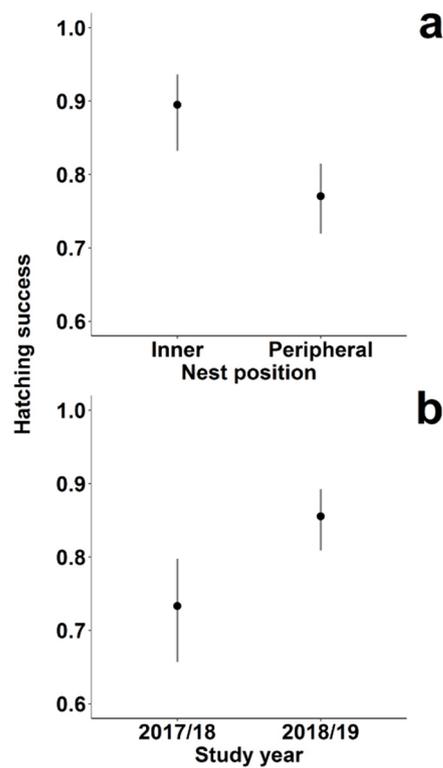


Figure 6. Effects of (a) nest position and (b) study year on the hatching success of Adélie penguins predicted by GLMs. Black dots: predicted values. Grey bars: 95% confidence intervals.

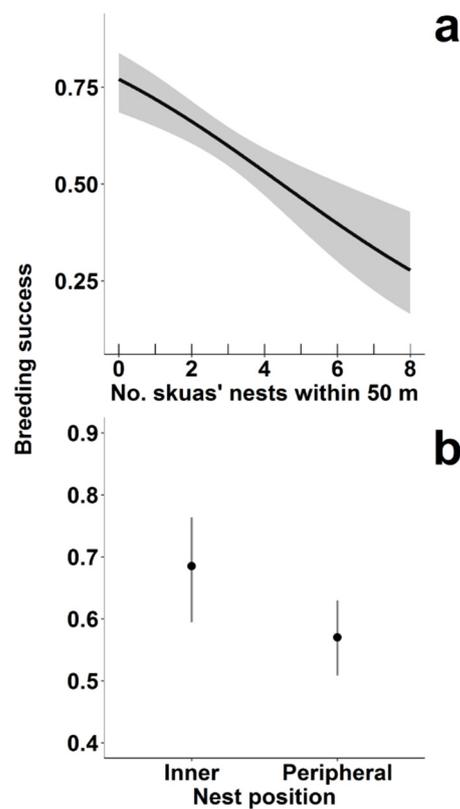


Figure 7. Effects of (a) number of skua nests within 50 m and (b) nest position on the breeding success of Adélie penguins predicted by GLMs. In (a), marks along the x-axis show the distribution of observed values. Black lines or dots: predicted values. Grey bands or bars: 95% confidence intervals.

3.3. Differences in Chick Growth between the Two Colonies

The body mass of chicks regularly sampled from study nests did not differ between the two colonies throughout the first month of life (LMM, coefficient estimates and 95% CIs: intercept = 6.631 [5.750, 7.514], colony EdPo = -0.007 [-0.131 , 0.117]; variances of random intercepts: sampling period = 0.667, nest identity = 0.035; Figure 8).

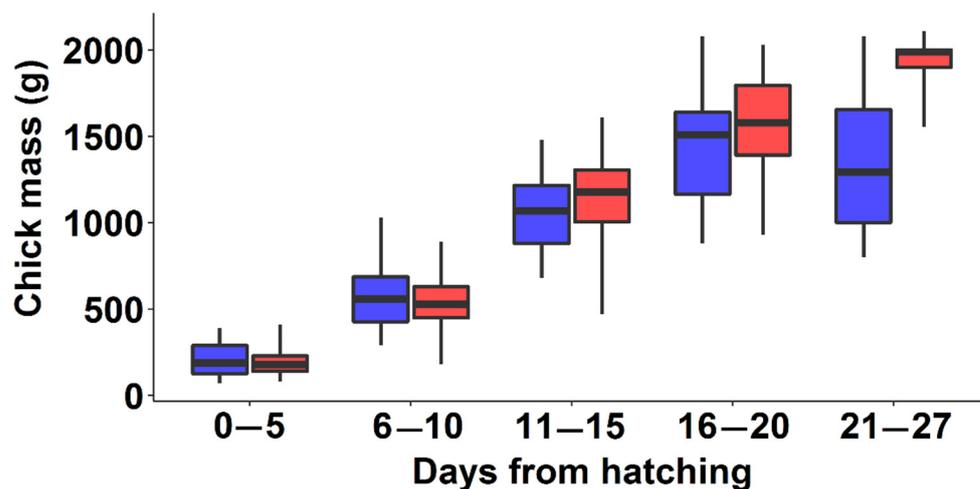


Figure 8. Observed chick mass (grams) within arbitrarily-defined periods spanning hatching to late guard stage in the two study colonies (blue: AdCo; red: EdPo). The modified boxplots show median (thick line) and range (whiskers) of observed values.

4. Discussion

Automated cameras and direct observations reported that main breeding events followed a similar chronology at AdCo and EdPo. Breeding chronology is in line with data reported for the same area [39,46] and elsewhere in the Ross Sea [44]. Our naïve estimation of breeding success was comparable among the three colonies and was consistent with previous studies [39,46]. Mean reproductive success measured from 16 breeding groups nesting at Esperanza Bay (Antarctic Peninsula) for eight seasons (1995–2004) averaged 1.02 chicks per pair [61] (range: 0.42–1.58). Further data collected all around Antarctica (12 different locations) and spanning 34 years (1959–1998) averaged 1.0 [44] (0.1–1.6; p. 151). EdPo breeding output reported in a previous study averaged 0.76 [46] (0.34–0.97, eight seasons, 1994–2005). Low values (below 0.5 chicks per pair) were generally reported by authors as “bad” years and ascribed to unusual weather/windchill conditions at the nest, extensive sea ice in front of the colony, lower meal size, or starvation of chicks [46] (for 2002/03); [62] (for 1995/96). Data recorded in our study can thus be considered aligned to mean values reported for Antarctica, indicating that Mid Victoria Land colonies did not show low reproductive success during our study period. Small differences in breeding success among the two years at EdPo and AdCo could be due to natural fluctuations possibly depending on several different drivers such as sea ice cover and food availability, competition for food or breeding areas [47]. Moreover, such inter-annual differences were not confirmed when we accounted for other factors affecting breeding success at the individual nest scale (see below).

Our study colonies are relatively close to each other but exposed to different local sea ice conditions and differ as much as tenfold in breeding population size. EdPo is generally separated from the sea by several kilometers of fast ice (Table 1). Conversely, the larger ones, AdCo and InIs, are located on Terra Nova Bay polynya, which plays an important role in facilitating access to foraging areas, reducing energy costs of traveling throughout the breeding season [25,39,41]. Colony size-dependent intraspecific competition can be high and can reduce food availability for chicks during the breeding season [63]. However, despite the larger colony size, a previous study has shown that chick mass during chick-

rearing was greater at InIs than EdPo, highlighting the importance of the Terra Nova Bay polynya as a foraging hotspot for penguins [39]. Data on meal mass and diet composition were not available for this study; nonetheless, the mass gained by chicks from hatching up to the crèche stage can indeed be considered an index of food supply [64]. One could have expected that chick mass was greater at AdCo than at EdPo due to differences in food accessibility/availability, yet chick growth during the 2018/2019 season showed no differences between EdPo and AdCo. Thus, independently of colony size and distance to fast ice, we suggest that food resources at sea were largely available to chick—rearing parents in both colonies during the 2018/2019 breeding season. The fact that chicks grew up at a similar rate and that breeding success was similar at both localities may also suggest that parents fed their offspring with similar proportions of fish and krill. Suggestively, the summer diet composition reported at AdCo and EdPo in previous years seems to confirm our hypothesis of a similar diet composition in these colonies [65].

Our analysis conducted at the nest level showed that penguin reproductive success is mainly influenced by the presence of neighboring skuas: the greater the number of skua pairs nesting 50 m around the focal penguin nest, the lower the chick survival probability. Interestingly, the effect of the number of skua nests within 100 m of the penguin nest was not supported by our best model, and in fact, a 50 m radius corresponds approximately to the size of skua feeding territories in another Ross Sea penguin colony [50]. Additionally, we found that the number of neighboring skuas did not affect hatching success, suggesting that skua predation is more successful at targeting chicks rather than eggs. Understanding the mortality causes of penguin eggs and chicks is often hard. The direct reason for the loss of the egg or chick can be rarely observed in the field, thus making the estimate of causes of egg loss/chick death difficult, which must be traced by analyzing different circumstances. Factors leading to the loss or non-hatching of an egg may range from non-fertility of the egg, abandonment of the nest or non-return to the nest by the parent, accidental release or squashing of the chick during adult fighting [66], or predation by skuas [35]. The causes of egg or chick loss also vary according to the period in which they occur and can also be found in the position of the nests in the colony and the degree of experience of the adults. In likelihood, egg incubation by parents makes egg predation by skuas more difficult than direct predation on chicks, which are mobile and less easily protected by adults. This is even more effective in central nests because skuas attack at ground level and prey better on peripheral nests [44,67]. Irrespectively of the occurrence of skua nests nearby, penguin reproductive success was influenced by nest location, with peripheral breeders being less successful than inner-nesting breeders. In colonial seabirds, peripheral nesting locations seem inherently less advantageous than interior ones [68,69]. As for the Adélie penguin, it has been suggested that nest location is related to the age/experience of the occupants, where more experienced or 'dominant' individuals occupy the central positions [48,70,71]. The fact that peripherals are "lower-quality" individuals is also suggested by their reduced hatching success, which is not affected by skuas [33,44]. In any case, the effect of nest position on breeding output may thus propagate at a larger scale, influencing the breeding success at the subcolony scale. Subcolonies with a high perimeter-to-area ratio should show lower breeding success due to a higher proportion of peripheral nests [34,48].

At-nest weather conditions may also influence penguin breeding success in several ways [21], yet the average windchill conditions experienced by chicks from birth until the measurement of their reproductive success did not affect their survival. Although the confidence interval of this predictor's coefficient overlapped '0', implying large uncertainty about its effect, we cannot rule out the importance of windchill because the occurrence in the top-ranked model suggests some degree of support in affecting breeding success. Most likely, future studies should re-evaluate this variable by considering a longer study period. Our dataset indeed spanned only two years and the associated windchill variability could have been narrow to allow the detection of significant effects. Moreover, unaccounted weather predictors (e.g., snow) might have been correlated to windchill, explaining its occurrence in the top-ranked model. Meteorological conditions at the nest were reported

among critical factors affecting chick survival at EdPo in the 2002/2003 breeding season [72]. Local weather events such as snowfall (or more rarely rain) could also have a negative effect on breeding success [32,73]. Unfortunately, data on these parameters were not available during our study period and therefore the effect of weather should be further verified by long-term data considering more meteorological parameters intimately linked to habitat suitability [72–74].

While accounting for nest-specific characteristics, breeding success did not differ between study years. Conversely, a higher hatching success emerged in 2018/2019, regardless of the colony, as well as heavier chick mass (see Figure S1, Supplementary Material) and earlier hatching occurred at EdPo in 2018/2019. Hatching success may vary across locations and years. Results for our colonies (ranging from 69% to 85% hatched eggs during our study; Table S1, Supplementary Material) agreed with the historical literature records ([44] p. 151, spanning 37% to 88% in 21 seasons; [46] spanning 58% to 86% in 8 seasons at EdPo). Since skua predation did not affect hatching success and the arrival dates at the colony were similar for EdPo, other factors such as harsher weather at the colony in the first season or fast ice extension may have contributed to later hatching and lower chick mass at EdPo in 2017/2018, as well as to lower hatching success in both colonies, possibly explaining these fluctuations between study years. A similar explanation has been proposed by a previous study conducted in the same area, when extensive fast ice in front of the colony forced parents to longer foraging trips and low hatching success was measured [39,46].

With other things being equal, our model showed that there were no general differences in reproductive success between the two colonies, further confirming results achieved through the naïve estimation of breeding success. Although the stressors hypothesized for penguins are inherently greater at EdPo than at AdCo (i.e., higher per capita skua predation pressure, persistent fast ice in front of the colony), our findings clearly support that local factors such as nest position and predation risk around the nest, and in turn, the quality of the nesting environment, seem more important than the general condition of the colony in determining the probability of chick survival. The number of neighboring skua pairs, which had the strongest effect size amongst other predictors, seems to be especially crucial for penguin breeding success [75]. In the long-term, skua numbers may thus be expected to be critical drivers of Adélie penguin population dynamics (see also [76] for southern rockhopper penguin *Eudyptes chrysocome*). For example, colonies with a higher skua predation pressure may be more impacted by future stochastic environmental events, as well as would be those with a higher perimeter-to-area ratio [34]. In addition to the effects of sea ice and marine productivity, which are already well known for this species, our work emphasizes how the variables related to the choice of the nesting environment within the colony are also crucial in determining the success of a predator which certainly depends upon marine habitat, but it is still obliged to nest in ice-free land. Furthermore, despite the fact that we did not find support for an effect of at-nest weather conditions on penguin breeding success, earlier research has shown that local weather, including snowfall/rain or stochastic regional meteorological events, can affect habitat suitability, contributing to a reduction in the annual breeding success or to anomalous breeding failure [72–74]. Therefore, future studies on the Adélie penguin should be conducted by considering jointly the effects of colony and marine habitat characteristics in order to disentangle their subtle effects on breeding success.

Understanding the importance of terrestrial factors in affecting the breeding output of a marine species that remains dependent on the land for breeding, rearing young, and molting [77] also offers some considerations on conservation issues. More and more often penguins and humans occupy similar habitats in Antarctica [78] and human activities can modify the terrestrial habitats and increase disturbance at breeding sites. Only 2% of the Antarctic continent is ice-free, and those areas mostly occur along the continent's coasts, allowing life in terrestrial ecosystems for well-adapted animals and plants. Increasing human pressure represents a future challenge for Antarctic terrestrial habitats [79]. The level of human disturbance to coastal flora and fauna is increasing at alarming rates, especially

in areas close to research stations, where main logistic activities are carried out [80]. Any habitat loss/shrinkage or disturbance such as those due to human infrastructures and activities may further interplay with such variables, impinging on the terrestrial habitat quality for nesting penguins, thus on their breeding output. Therefore, we suggest that the characteristics (natural and/or affected by human activities) of the terrestrial environment should be integrated and must be also duly considered for the planning of management and conservation of marine birds and MPAs. Remotely operated instrumentation, such as time-lapse cameras, can be a valuable tool to integrate field data collected by researchers while reducing human impact. Long-term monitoring programs on indicator, sensitive Antarctic species need to be actively maintained by national Antarctic programs to provide scientific information that could help research and monitoring of Marine Protected Areas.

Supplementary Materials: The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/d14060429/s1>. Figure S1: Observed chick mass at EdPo colony in the two study years; Table S1: Mean breeding parameters of the Adélie penguins at Edmonson Point and Adélie Cove during two breeding seasons.

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Data Availability Statement: The data that support the findings of this study are available from the corresponding author, [SO], upon reasonable request.

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