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RESEARCH

I need some space: solitary nesting Adélie penguins demonstrate an alternative breeding strategy at Cape Crozier

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Abstract

According to the 'selfish herd' hypothesis, most seabird species breed colonially so that individuals can decrease their risk of predation by forming compact groups. However, costs and benefits associated with colonial breeding may not be evenly distributed among individuals within a colony. At Adélie penguin colonies, individuals nesting on the periphery of subcolonies (distinct groups of nests) may experience higher rates of nest predation by south polar skuas, and thus the optimal aggregation pattern for Adélie penguins may be within groups that minimize the proportion of edge nests. Nevertheless, some penguins choose to nest solitarily, at significant distances from conspecifics. We tracked 50 of these "solitary-nesting" Adélie penguins at Cape Crozier, a large colony on Ross Island, during the 2021 nesting season and compared their breeding success to individuals nesting within subcolony boundaries. We found that both solitary and subcolony nests successfully raised chicks large enough to join crèches and left unattended by adults. However, chicks from solitary nests exhibited a rate of mortality more than six times higher during the transition from nest brooding/guarding to crèche stage. In the 2022 nesting season, we found that solitary nests which had previously hosted actively breeding penguins were more likely to be re-occupied. Solitary nesting therefore appears to be a less-successful alternative to breeding within subcolonies, but enough individuals could be successful with this approach to maintain the apparently disadvantageous behavior and effectively pioneer previously unused locations, possibly including eventual new colony locations.

Keywords Colonial breeding · Nest predation · Selfish herd · Breeding success · Habitat pioneering

Introduction

Colonial breeding is nearly ubiquitous among seabirds, having been recorded in more than 90% of seabird species (Lack 1967; Coulson 2002). Though apparently adaptive on evolutionary time scales, the costs and benefits of coloniality may vary among species and individuals across space and time (Wittenberger and Hunt 1985). Most seabirds depend on terrestrial nesting space in close proximity to marine prey resources, which may influence the selection of colony locations and limit colony size (Alexander 1974; Forbes et al. 2000; Ainley 2002). However, considerable variation in the distribution and size of seabird colonies within areas of suitable habitat implies the existence of driving forces beyond habitat limitation (Furness and Burkhead 1984; Wittenberger and Hunt 1985; Brown 2016; Santora et al. 2020).

Patterns of colonial breeding are likely to be driven by selection across various life-history dimensions, including risk of predation and access to resources. For example, individuals may choose to breed in aggregations to reduce their individual risk of predation (Hamilton 1971). Under this 'selfish herd' hypothesis, individual risk of predation can be reduced through swamping predators' ability to exploit an entire population (Patterson 1965; Nisbet 1975; Williams 1975) or through group vigilance and defense tactics which directly reduce the effectiveness of predation attempts (Treisman 1975; Williams 1975). Additional benefits of coloniality include benefits from group foraging and public information (information gleaned from conspecifics, either through observation or communication) (Boulinier et al. 1996; Cook et al. 2017). In polar climates, social thermoregulation (huddling), either by adults, in the case of Emperor penguins, or by chicks forming crèches, can also provide important benefits (Black et al. 2016; Gilbert et al. 2006). Simultaneously,

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large aggregations of organisms with identical ecological needs are likely to increase competition where available resources are limited. Such competition may manifest through direct interactions (such as increased aggression, territory disputes, and nest theft) (Williams 1942; Stonehouse 1962; Burger 1978) as well as indirect interactions (such as resource depletion around the colony) (Ashmole 1963; Birt et al. 1987; Ainley et al. 2004). Tradeoffs such as these shape colonial behavior at the individual as well as species level (Wittenberger and Hunt 1985).

Adélie penguins (*Pygoscelis adeliae*) are one of two penguin species that breed only in Antarctica, and likely experience strong selection toward coloniality due to extreme limitation of suitable habitat. Breeding Adélie penguins require terrain free from ice and snow (available across < 5% of the Antarctic coastline), which must also have abundant stones for nest building, near both open water and sea ice (Ainley 2002). The size and distribution of many Adélie penguin breeding colonies are well-documented, and several colonies are the subject of long-term monitoring efforts (Lynch and LaRue 2014; Santora et al. 2020). Cape Crozier, the largest of three Adélie penguin colonies located on Ross Island, has been studied continuously since 1996, during which time it has grown substantially from ~ 170,000 breeding pairs to > 270,000 breeding pairs in 2014 (Ainley et al. 1995; Lynch and LaRue 2014; Lyver et al. 2014).

Within Adélie penguin breeding colonies, nests occur in distinct groups, referred to as subcolonies. Habitat quality of discrete subcolonies (and even nests within subcolonies) is highly variable. Some evidence suggests that breeding success within a subcolony is best predicted by its shape and size, affecting the proportion of penguins in the group located along the periphery (Schmidt et al. 2021). Chick predation by south polar skuas (*Stercorarius maccormicki*) is higher on peripheral nests, and is one hypothesized driver of this pattern (Tenaza 1971; Davis 1982; Schmidt et al. 2021). Because they have fewer neighbors to signal and guard against intruders, peripheral nests may be more vulnerable to ground as well as aerial attacks. Together, these data suggest that the optimal distribution of Adélie penguin nests is in the interior of large, circular subcolonies; however, some penguins do not follow this pattern. Across colonies, a small subset of Adélie penguins nest solitarily, separate from any subcolony group. Some evidence suggests that solitary nesting penguins are primarily inexperienced breeders with low breeding success (Tenaza 1971). However, any solitary nests which do successfully raise chicks may be perceived as alternative habitats and attract other penguins to occupy new areas (Danchin et al. 1998; Kildaw 1999). To date, the breeding success and re-occupancy among solitary nests have not been fully explored.

In this study, we evaluated the selfish herd hypothesis from the perspective of individuals who go it alone. To evaluate solitary nest breeding success, we tracked Adélie penguins in 50 solitary and 102 subcolony nests at Cape Crozier during the 2021 breeding season and compared the quantity and size of chicks from each clutch before and after chicks left their parent's nest. We considered three predictions related to breeding success: (1) solitary nests should produce fewer crèched chicks on average compared to nests located within subcolonies; (2) Solitary nests should be located near habitat features which reduce their exposure if predation is a primary driver of reduced success; and (3) solitary nests should produce smaller chicks than those within subcolonies if solitary nests are primarily occupied by inexperienced breeders (Tenaza 1971). Based on previous research suggesting that seabirds may select breeding habitat based on perceived conspecific success (Danchin et al. 1998), we also predicted that solitary nests which successfully raised chicks to the crèche stage would be re-occupied more frequently in the subsequent breeding season.

Methods

Study site

The study was conducted at Cape Crozier (77°27′S, 169°14′E), Ross Island, Antarctica (Fig. 1). Adélie penguins arrive between late October and early November to claim territory, construct a pebble nest, form pairs, and mate. Females lay one or two eggs in November, and parents take turns attending and incubating eggs for about 35 days (Taylor 1962; Ainley 2002). Newly hatched chicks are constantly attended by at least one parent for about 20 days, also known as the brood stage (Ainley 2002; Jennings et al. 2023). Once chicks are thermally independent and growth cannot be sustained by the foraging of only one parent, chicks are left unattended and form groups called crèches, while both parents forage at once (Davis 1982).

Nest tracking

To address our hypotheses about breeding success, we compared the number of chicks surviving per nest, among Adélie penguins in solitary and subcolony nests. Solitary nests were defined as any nest greater than 3 m (~ 3 times the average inter-nest distance, calculated from 35 nests selected using a random point generator in an aerial orthomosaic with ~ 1 cm per pixel resolution) from the nearest subcolony. During the 2021 austral summer, we monitored the breeding success of 50 solitary nests distributed throughout the colony at Cape Crozier (Fig. 1). Here, we refer to breeding seasons using the initial year of the season (i.e., the summer of 2021–2022 is referred to as the 2021 season). We identified the 50 solitary nests during three surveys of the colony in mid-November, after which nests were photographed, a marker was placed within 15 cm of each nest, and the habitat features (such as large rocks) and GPS positions were recorded to facilitate relocation. Only sites which showed at least some nest construction (demonstrated by pebble accumulation) were selected.

Over the course of the 2021 season, nests were checked every four to seven days to monitor the development and survival of chicks from each nest. Observations were made using binoculars, standing ~ 5 m from the nest to minimize disturbance. On each check, we recorded breeding status (incubating, brooding, or crèched), nest contents (number of eggs or chicks), as well as chick size once hatched (size categories described below, Table 1). On each check (and especially approaching the transition from one breeding status to another), observers waited until penguins stood or shifted to clearly view nest contents. For nests that were first seen attended by an adult but with no eggs, we returned every four days to check for eggs. If no egg was seen in the nest by the time of median hatching within the colony (when half of observed eggs had hatched), that nest was defined as non-breeding and dropped from the study. Among monitored solitary nests, median hatching occurred on December 23th in 2021. For nests that were seen with one or more eggs, we returned once every seven days until the egg(s) hatched. After hatching, we visited nests every four days and visually estimated chick size as a fraction relative to the flipper length (FL) of the attending adult, assigning each chick to a size category between 0 and 6 (Table 1). Once chicks from a solitary nest were determined large enough to potentially enter a crèche (chicks at least size class 1, the size when > 75% of historically monitored subcolony chicks entered crèches; this study), a strip of black tape (4651 Tesa®, Norderstedt, Germany) approximately 1 by 3 cm was attached to a pinch of down on the back of the chicks as a marker to track them as they moved from their natal nest to a crèche. Some tape strips were given unique white (paint pen) or silver (duct tape) markings to visually differentiate between different chicks from solitary nests in the same area. We stopped visiting study nests if they were empty on two consecutive checks before chicks reached the size threshold for marking (recorded as a failed nest). For chicks which met size criteria (class 1 or larger) and were marked when last seen in a nest, we attempted to locate them within nearby crèches on two consecutive checks, where re-located chicks were designated successful and chicks that were never re-sighted in a crèche were designated as failed.

Table 1 Size categories used to classify Adélie penguin chicks which met our brood success criteria

Size category	Size relative to adult FL (%)
0	< 50
1	50–62.5
2	62.5–75
3	75–87.5
4	87.5–100
5	100
6	> 100

Size categories were assigned by visually comparing the chick's body size (excluding head and neck) to the flipper length (FL) of the bird that was brooding the chick

As part of an ongoing demographic study, subcolony nests (defined as any nest within 1 m of at least two other actively breeding Adélie penguins) in which one parent was flipper-banded, were monitored in 2021 through the brood stage. Chicks from these nests were not marked so we were not able to follow them into the crèche or determine chick survival beyond the brood stage for subcolony nests in 2021. However, chicks were marked as part of a separate, previous study (in 2016–2019), where nests of flipper-banded adults across 49 subcolonies were monitored (Table 2). Flipper-banded penguins on active nests were located in early November of each season, at which point nests were flagged and checked every 4–7 days following the same protocol described for solitary nests. During the 2016–2019 breeding seasons, chicks from subcolony nests were marked approximately 2 weeks after hatching using an individually numbered plastic T-bar "fish tag" (Floy Tags Inc., USA) anchored subcutaneously (Jennings et al. 2016). These markings allowed us to re-locate chicks during the crèche stage and marked chicks were ultimately recaptured at the end of the breeding season to remove their tags.

Success metrics

To assess our first prediction, we compared the breeding success of solitary and subcolony nests at two key points during the breeding cycle. The first metric, brood success, represented the number of chicks that survived the brood stage and disappeared at a size large enough to have potentially entered a crèche (e.g., at or above size class 1). Only chicks which exceeded this size threshold before disappearing from

Table 2 Sample sizes of subcolony nests (one parent flipper-banded) tracked at Cape Crozier from 2016–2019 and 2021 used in this study

Breeding season	Number of tracked nests
2016	80
2017	52
2018	51
2019	28
2021	102

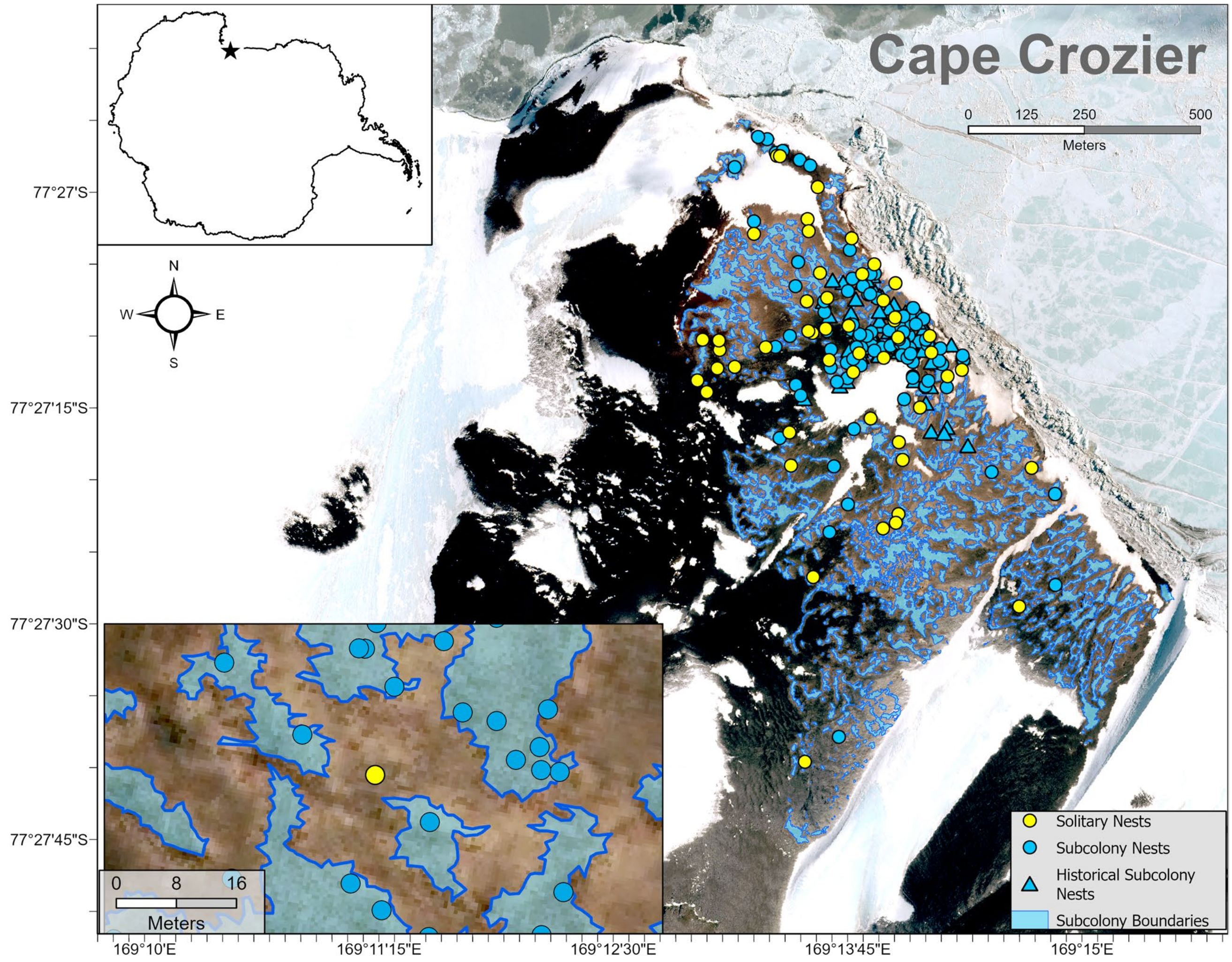

Fig. 1 Map of tracked nests at Cape Crozier, Ross Island, Antarctica. Locations of solitary nests within the colony are shown in yellow and subcolony nests are shown in blue. The star on the upper inset map of Antarctica indicates the location of Ross Island. Close-up, bottom inset shows spatial segregation of solitary and subcolony nests with boundaries of subcolony areas shaded in blue. Satellite image of Cape Crozier from WorldView-3, November 20, 2014 (copyright 2014 DigitalGlobe, NextView License)

their parent nest were designated successful. We used a Wilcoxon rank-sum test to compare the number of chicks which met brood success criteria between solitary and subcolony nests (Wilcoxon 1945). One advantage of using brood success as a metric is that it can be determined without requiring chicks to be physically marked. We therefore have a brood success outcome for all chicks from tracked nests and can make a statistical comparison of subcolony and solitary nests based on direct observations from the 2021 season. However, brood success does not account for mortality during the transition to the crèche stage. Our second metric, crèching success, represents the number of chicks confirmed to have survived to enter crèches. Under this metric, only chicks observed at least once within a crèche were designated as successful while any chicks which disappeared before reaching size class 1 (and were therefore unmarked), or which were never re-sighted in a crèche were assumed to have died. Crèching success is a more accurate measure of breeding success since it accounts for chick mortality during the transition from brood to crèche stage, but requires that chicks be marked (distinguishing individuals within groups) which we did not do for subcolony nests in 2021 (therefore we lack an estimate of this value from 2021, Fig. 2). Instead, we used values of brood and crèching success from historical subcolony nests to calculate an estimate of “expected” crèching success for subcolony nests in 2021. This was achieved by calculating the average difference between brood and crèching success in each year, which we refer to as transition mortality, given it represents the number of chicks which survived through the brood stage but then died during the transition to the crèche.

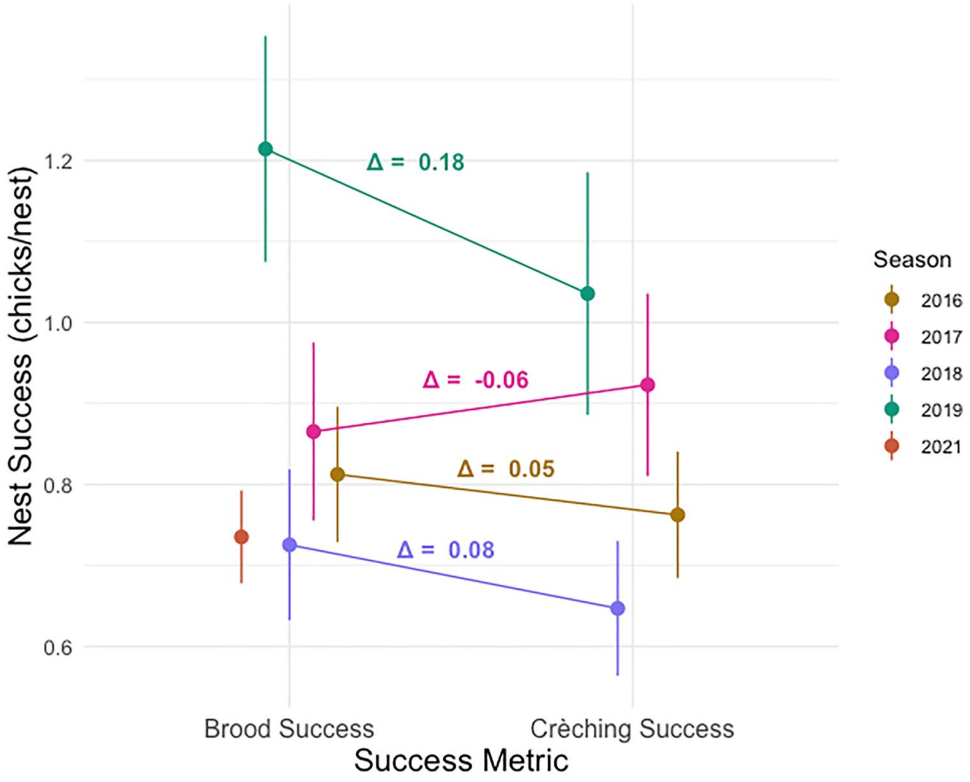

Fig. 2 Brood and crèching success values for historical and contemporary (brood success only) subcolony nests. Transition mortality (Δ) is the difference between crèching success and brood success, and is shown above each line. Crèching success could not be observed for subcolony nests in 2021 because chicks were not physically marked. Historic values of transition mortality shown here were used to estimate crèching success for subcolony nests in 2021 (Fig. 3). The negative transition mortality in 2017 (which had higher than average breeding success) was due to three chicks that were last seen at size class 0 (designated as failed under brood success criteria) but later found in crèches (designated as successful under crèching success criteria)

Calculating transition mortality allowed us to control for interannual variability when estimating crèching success. In Adélie penguin colonies, the number of chicks that survive to crèche varies naturally between years based on environmental conditions, and therefore, the exact values of brood and crèching success from previous seasons cannot be directly compared to values from 2021 (Dugger et al. 2014). By comparison, our data show that values of transition mortality have a much smaller range of interannual variation among subcolony nests (Fig. 2). Therefore, applying a historic average of transition mortality is likely to produce a reasonable estimate of crèching rates in 2021. Including both brood and crèching success allowed us to compare the number of chicks that died during the transition from the brood to crèche stage for solitary and subcolony nests.

To estimate crèching success for subcolony nests in 2021, we first determined the difference between average crèching success (CS) and brood success (BS) for subcolony nests tracked during the 2016–2019 seasons (Fig. 2). This difference is hereafter referred to as the transition mortality ($\mathrm{TransitionMort}_{\mathrm{year}}$).

$$\mathrm{TransitionMort}_{\mathrm{year}} = \mathrm{mean}(BS_{\mathrm{i}}) - \mathrm{mean}(CS_{\mathrm{i}})$$

where i represents an individual nest in a given year. Next, we used these estimates of transition mortality from all four years of historical subcolony data to calculate a range of expected crèching success values for 2021 based on the observed brood success.

$$Expected\ SubcolonyCS_{2021} = \mathrm{mean}(BS_{2021\mathrm{i}}) - \mathrm{TransitionMort}_{\mathrm{year}}$$

These four expected subcolony crèching success values for 2021 were then compared with the mean observed crèching success and transition mortality for solitary nests. Because we are only able to estimate crèching success for subcolony nests based on historical data, we refrained from making a statistical comparison of crèching success between solitary and subcolony nests as we did for brood success.

To assess our second prediction relating to breeding success, we tracked the number of solitary nests located next to a large shelter rock. Here, shelter rocks are defined as any rock > 15 cm in diameter which blocked access to the nest on at least one side. We hypothesized that solitary nests would be preferentially located next to such shelter rocks because they could improve solitary nest success by reducing the angles from which solitary nests were vulnerable to attacks by predators.

To assess our third prediction relating to breeding success, we evaluated the size of chicks from solitary and subcolony nests when last seen in their natal nest. Chick survival is heavily influenced by size, and chicks that attain larger sizes before entering crèches are more likely to survive to fledging (Jennings et al. 2023). We used a chi-square test to determine if the distribution of chick sizes (Table 1) were different between solitary and subcolony nests at the last observation before chicks left their natal nest. To further test our hypothesis and determine if differences in chick size might be attributable to differences in parental investment between solitary and subcolony nests, we compared the length of the brood stage for chicks from each nest type. We calculated the length of the brood stage for each chick as the difference between median hatch date in 2021 (the day when half of tracked nests had hatched chicks) and the date when each chick was last observed in their natal nest. Owing to the four-day interval between nest checks, we could not determine a precise hatch date for each chick and used a median hatch date instead. The median hatch date for solitary and subcolony nests was December 23 and 24th, respectively. We used a Student's t-test to determine if brood duration differed between nest types. Finally, we fit an ordinal regression model predicting chick size by brood duration and nest type to explore if either variable could explain observed differences in chick size.

To address our prediction about solitary nest re-occupancy, we revisited solitary nest sites in mid-November to late December of the following season (2022). Each solitary nest was visited at least twice and, if a penguin was present on at least one of these checks, the nest was considered to be reoccupied. We compared the number of solitary nests which were re-occupied in 2022 based on their breeding status and outcome in 2021 to assess if re-occupancy could be predicted by performance in the previous season. Specifically, we used a Fisher's exact test to compare the number of nests re-occupied or not between solitary nests which successfully raised chicks and those which did not. We conducted our Fisher's exact test first using data from all solitary nests which were occupied in 2021 and again using only those which were actively breeding in 2021. We used both brood and crèching success for this comparison to determine if success in one stage of the breeding cycle is more important to nest re-occupancy than another. All analyses were conducted using R v4.2.1 (R Core Team 2022). Means are presented ± the standard error unless otherwise noted.

Results

Nest monitoring effort

Of the 50 solitary nests we monitored in 2021, 36 (72%) were ever seen with eggs or chicks (i.e., were "active"). The number of subcolony nests followed each year ranged from 28 (2019) to 102 (2021) and was distributed across > 40 distinct subcolonies (Fig. 1). Nest locations for solitary nests were more widely distributed throughout the colony than subcolony nests in 2021 (Fig. 1).

Breeding success

Brood success

In 2021, 23 of 36 active solitary nests produced chicks of at least size class 1, which met our size criteria for brood success and were assumed to be large enough to enter a crèche. Of these 23, four nests raised two chicks to at least size class 1 and 19 nests raised one chick. This resulted in an average brood success of 0.75 ± 0.11 chicks for solitary nests. In the same year, 102 active subcolony nests were tracked and 68 produced chicks that survived the brood stage. Of these 68, seven nests raised two chicks and 61 nests raised one yielding an average brood success of 0.74 ± 0.06 chicks per subcolony nest. We found no difference between brood success of solitary and subcolony nests (Wilcoxon rank-sum test, $W = 1831$, $p = 0.98$; Fig. 3).

Crèching success

In total, 11 out of 36 solitary nests raised chicks that were directly confirmed to enter a crèche. Of these, one nest raised two chicks to crèche, while 10 raised only one. From these data, we calculated an average crèching success rate of 0.33 ± 0.09 chicks per solitary nest, less than half the brood success estimate. The transition mortality for solitary nests was 0.42 ± 0.09 chicks lost per nest between the brood and crèching success estimates. By comparison, transition mortality among historical subcolony nests ranged from − 0.06 to 0.18 chicks per nest (average 0.06 ± 0.04). Based on these data, the magnitude of mortality experienced by chicks from solitary nests was 6.69 times higher on average than among subcolony nests during the transition between brood and crèche stages. Using our historical values of transition mortality, the mean expected crèching success for subcolony nests in 2021 was 0.67 chicks per nest and estimates based on individual years ranged from 0.56 to 0.79. These estimates suggest that solitary nests produce 42–60% (mean 50%) fewer chicks entering the crèche stage compared to subcolony nests.

While the solitary nests monitored in this study were widely distributed throughout the Cape Crozier colony, most were located near a common habitat feature. We observed that 36 of the 50 solitary nests we originally identified (including 26 active solitary nests) were located next to a large rock (≥ 15 cm in diameter). Rocks ranged in size from 15 to 150 cm in diameter and provided shelter by reducing the area of exposure on at least one side of the solitary nest.

Among chicks that met the brood success criteria, chicks of solitary nesting penguins were last seen at their nest at larger sizes compared to chicks from subcolony nests in 2021 (Fig. 4; chi-square test, $\chi^2 = 30.5$, $p < 0.001$). Approximately, 30% of chicks from solitary nests belonged to the

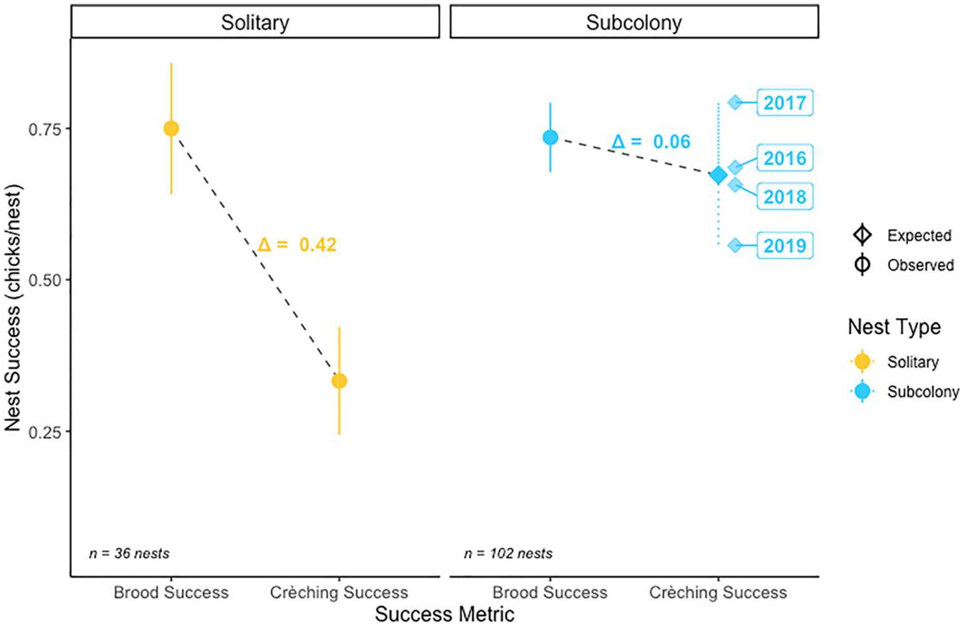

Fig. 3 Brood and crèching success among solitary (yellow) and subcolony (blue) nests in 2021. Center points represent the mean for each group, while solid error bars extend one standard error in either direction. Four values of expected crèching success were generated for subcolony nests in 2021. These were calculated as the difference between observed brood success from 2021 and transition mortality values from subcolony nests monitored in four historical breeding seasons (Fig. 2). Mean expected crèching success is presented in bold with a dotted error line displaying the range values. Individual values of expected crèching success are also displayed offset and in a lighter shade. Expected crèching success values calculated using historical data are shown as diamonds, while data directly observed in 2021 are plotted as circles. The number of solitary and subcolony nests tracked in the 2021 season are provided in the bottom left corner of each plot, while sample sizes of historical subcolony nests used to calculate crèching success estimates are found in Table 2. The difference in brood and average crèching success (transition mortality) is printed above the black dashed connecting lines

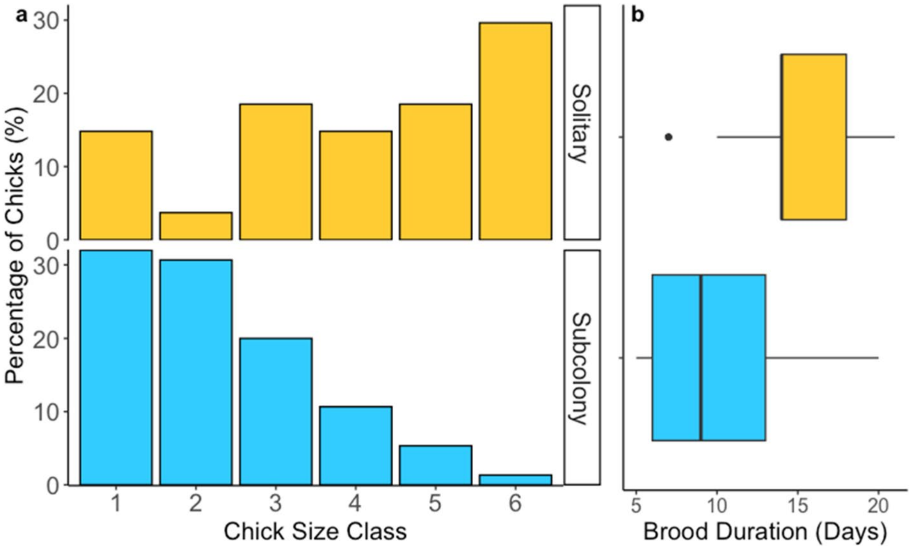

Fig. 4 **a** Size distribution of chicks which met brood success criteria in 2021 from solitary (yellow) and subcolony (blue) nests. Chick sizes are estimated relative to the size of an adult penguin flipper and placed in binned classes (Table 1). **b** Summary of brood duration measured as days since median hatch when chicks were last seen in their natal nest (Median hatch for solitary nests: 12/23/2021; subcolony nests: 12/24/2021)

largest size class (> 100% of adult flipper length) before disappearing from their natal nest, while only 1% of subcolony chicks reached this size before entering crèches. By comparison, the largest fraction of subcolony chicks (32%) disappeared at the smallest size required to meet the brood success criteria (50% of adult flipper length). Chicks from solitary nests disappeared from their natal nest 4 calendar days (95% CI = 2–6 days) later on average compared to chicks from subcolony nests (Student's t-test, $t = -4.75$, $p < 0.001$; Fig. 4). However, an ordinal regression model suggested the difference in size between chicks from solitary and subcolony nests was not attributable to a difference in brood duration ($p = 0.63$) Nest type was the only significant predictor of chick size ($p < 0.01$) in our model.

Re-occupation rates

In 2022, we re-located 41 of the solitary nests tracked in 2021. The remaining nests either could not be re-located ($n = 3$), or the identity of the original solitary nest was ambiguous ($n = 6$). Among re-located nests, 20 (49%) were re-occupied, all of which were among the 36 nests which hosted active breeders in 2021. We made our statistical comparison using all occupied solitary nests in 2021 which were re-located in 2022 ($n = 41$) as well as using only solitary nests that were active (confirmed to have an egg or chick) in 2021 and re-located in 2022 ($n = 34$). When occupied nests from 2021 were considered, nests that raised chicks through the brood stage in 2021 ($n = 23$ nests) were three times more likely than those which did not ($n = 18$) to be re-occupied the following season (Fisher's Exact test, $p = 0.003$). However, when testing across only nests that were active in 2021 and re-located in 2022, nests that raised chicks through the brood stage ($n = 23$) were not significantly more likely to be re-occupied than those that failed earlier ($n = 11$; Fisher's Exact test, $p = 0.058$). When using crèching success criteria instead of brood success ($n = 11$ successful nests), there were no significant relationships between outcome in 2021 and re-occupancy in the subsequent season among either nests which were occupied or those which were active in 2021. Classifying ambiguous nests as re-occupied (vs. leaving them out) did not change the significance of our results. We also observed that four solitary nest sites from 2021 had attracted neighbors and were the locations of newly established, potential subcolonies (three or more active territories in close proximity in 2022).

Discussion

Breeding success

We found that solitary and subcolony nests appeared to have similar success through the brood stage but that substantially fewer chicks likely reached crèches from solitary nests than from subcolony nests. These disparate outcomes suggest that chicks from solitary nests experience a key mortality bottleneck during the transition from the brood to crèche stage. The most likely cause of this bottleneck is differential rates of predation by south polar skuas, despite the larger size of chicks from solitary nests at the end of the brood stage.

Solitary nest chicks likely become more vulnerable to predation relative to subcolony nests as the breeding season progresses. Adélie chicks are susceptible to skua predation during both the brood and crèche stage, until approximately 30 days of age by some estimates (Davis 1982). During the brood stage, chicks increase in vulnerability as they grow, becoming unable to fit completely under their parents or within the nest, making them easier for skuas to grab (Young 1994). Larger chicks are also more challenging for skuas to carry in flight, so as the season progresses, predation pressure shifts toward peripheral nests which are exposed to ground attacks (Young 1994). During the crèche-stage, skua predation is most effective on isolated chicks (Sladen 1958) especially those leaving crèches to solicit food from parents at their natal nest (Taylor 1962; Penney 1968). Solitary nests in this study were located more than 3 territories away from their nearest nesting neighbor, and therefore, chicks from these nests were exposed for longer periods when moving between their nest and the nearest crèche (Sladen 1958). Consequently, solitary nest chicks that disappeared during the transition from brood to crèche stage likely died from predation.

Solitary nesting penguins appear to be less affected by their increased vulnerability to predation during the brood stage, suggesting they may modify their behavior to overcome some of the inherent disadvantages of their isolated positions. For example, solitary nesting penguins may recognize an increased vulnerability to predators and select habitat features to strengthen their defensive positions in the absence of neighbors. We observed that 72% of solitary nests were positioned next to a large sheltering rock, which reduced exposure by obstructing at least one side of the nest. This percentage was the same among all occupied solitary nests and among only those which were actively breeding. The frequent association between solitary nests and sheltering rocks suggests their habitat selection is non-random and future work could use aerial imagery to map solitary nests and describe their association with these and other observable habitat features (Schmidt et al. 2021; Hinke et al. 2022).

In addition to selecting special habitat, solitary nesting Adélie penguins may partially mitigate the risk of predation by increasing their parental investment to raise larger chicks. Chicks which grow faster and attain larger sizes before entering crèches are more likely to survive to fledging and recruit to the colony as subadults (Chapman et al. 2011; Ainley et al. 2018; Jennings et al. 2023). Adélie penguins could raise larger chicks either by extending their brood period and/or providing more or higher quality food. While it did not appear that chick size was related to date of the last sighting at the nest, we could not formally test for a relationship in chick age on last sighting as we were not able to precisely determine hatch date. Previous research has shown that male Adélie penguin chicks grow faster than females and are fed more Antarctic silverfish (*Pleuragramma antarcticum*) (Jennings et al. 2021) and thus differences in provisioning behavior may be another cause of the observed size difference.

Alternatively, chicks from solitary nests may be larger because penguins in solitary nests are unable to effectively guard two chicks, and when one chick perishes, more energy is invested in the survivor. Out of 36 active solitary nests, we observed that 15 nests only succeeded in hatching one chick and of the 17 nests that hatched two chicks, one had died within 10 ± 1.64 days of hatching on average. This supports the hypothesis that solitary nests are extremely vulnerable to predation, and are only able to raise large chicks during the brood stage because they are quickly forced to invest all energy in guarding and provisioning a single chick, and often still predated during the transition to the crèche stage.

We have previously found that flipper-banded individuals at Cape Crozier averaged 8% longer-duration chick-provisioning trips than un-banded individuals (Dugger et al. 2006), which could lead to lower breeding success. Given that in this study we found that solitary nests have significantly lower crèching success than subcolony nests (where one parent was flipper-banded), the negative effects of solitary nesting could be larger than we report here. To further clarify the effects of solitary nesting, and also to address related ethical considerations, we recommend that future studies explore the use of alternative methods of marking the penguins (e.g., RFID tags; Ballard et al. 2001, Dugger et al. 2006).

Solitary nest persistence

We found evidence that some solitary nests do persist over time, despite significantly lower breeding success than their subcolony counterparts. All solitary nests we re-located had hosted active breeders in the 2021 season, suggesting only solitary nests that at least initiated incubation are likely to persist in future years. We also found some evidence that solitary nests that successfully raise chicks are more likely to be re-occupied than those which did not. However, this result was not significant when only active solitary nests were considered, suggesting that whether breeding was attempted is more important than breeding outcome when predicting solitary nest re-occupancy. In this study, we cannot quantitatively distinguish between new and returning occupants because solitary nesting adults were not physically marked, and therefore we can only speculate on the drivers of this pattern.

Additional studies tracking individual penguins in solitary nests across seasons are needed to determine the precise mechanisms driving solitary nest persistence. One hypothesis is that inactive solitary nests are abandoned more frequently because they are occupied by young penguins prospecting territory. Tenaza (1971) hypothesized that most solitary nests are occupied by young, inexperienced breeders, which are also more likely to wander the colony, claiming territories and pairing for short periods without attempting breeding (Ainley 2002). Indeed, we observed inactive solitary nests were, on average, abandoned 9 ± 1.5 days after they were first observed. Inactive nests may also be occupied by low-quality birds which do not return because they are less likely to survive to the subsequent breeding season relative to active breeders (Lescroël et al. 2009). Alternatively, active solitary nests may be occupied by older individuals which demonstrate greater breeding skill and stronger philopatry to their chosen territory (Ainley 2002). None of these hypotheses are mutually exclusive and future studies might evaluate them by marking adults at solitary nests using RFID tags (see above under Breeding Success) so that individuals can be distinguished between years. In any case, our results show that some solitary nests are able to persist over time, either by retaining their occupants and/or attracting new ones.

Significance of solitary nesting

Solitary nests produced chicks large enough to enter crèches and were consistently occupied over time, suggesting this strategy may allow Adélie penguins to colonize new suitable habitats. Climate warming is exposing new breeding sites for Adélie penguins along the Antarctic coast, while decreasing the northern extent of their sea-ice habitat (Emslie et al. 2007; LaRue et al. 2013; Lee et al. 2017). These shifts create the potential for a redistribution of the Adélie penguin global population (Forcada and Trathan 2009; LaRue et al. 2019; Wethington et al. 2023) and indeed colonies in the Ross Sea region (where the world's southernmost colonies are located) have grown substantially in recent decades (Lynch and LaRue 2014). However, given that solitary nesting is less successful than nesting in subcolonies, the prevalence of this behavior may instead signal shifts in resource competition and population dynamics within Adélie penguin colonies.

Indeed, seabirds become more likely to colonize new areas as the costs of occupying existing habitat exceed perceived risk of pioneering new territory (Forbes and Kaiser 1994; Tims et al. 2004; Kildaw et al. 2005). During periods of colony growth, density-driven competition for shared resources like prey (Ballance et al. 2009; Ainley et al. 2018) or nest materials (Carrascal et al. 1995; Morandini et al. 2021) may drive Adélie penguins to increasingly pioneer new habitat at the colony and subcolony scale. Furthermore, high nesting philopatry among Adélie penguins (Ainley 2002) ensures that young, inexperienced individuals are more likely to pioneer new territory (Coulson and White 1958; Blus and Keahey 1978). Therefore, shifts in solitary nesting behavior may be likely during periods of population growth, reflecting influxes of young birds and/or declines in existing habitat quality.

In theory, solitary nests which persist over time while also attracting new recruits may act as precursors in the process of subcolony formation. We observed four novel subcolonies appear at locations previously occupied by solitary nests, which supports this hypothesis. However, two of these subcolonies occurred at solitary nests which had not previously hosted active breeders. When considered with our other results, this observation suggests that while solitary nests may indeed act as precursors to subcolony formation, the drivers of this process are likely different (and perhaps independent) from those predicting solitary nest re-occupancy. Future research is needed to explore the connection between solitary nesting and population dynamics at Adélie penguin subcolonies.

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Author contribution AS, DK, and GB conceived and designed the study. AS, AL, and GB acquired funding and logistic support. AS and ME led the field team and all authors contributed to data collection. AC and AS analyzed the data. AC wrote the manuscript. All authors provided edits and approved the manuscript.

Data availability All data generated or analyzed during this study are included in a public repository hosted by Github, https://doi.org/10.5281/zenodo.8284755.

Declarations

Competing interests The authors have no relevant financial or non-financial interests to disclose.

References

Ainley DG (2002) The Adélie penguin: bellwether of climate change. Columbia University Press, New York

Ainley DG, Nur N, Woehler EJ (1995) Factors affecting the distribution and size of Pygoscelid penguin colonies in the Antarctic. Auk 112:171–182. https://doi.org/10.2307/4088776

Ainley DG, Ribic CA, Ballard G et al (2004) Geographic structure of Adélie penguin populations: overlap in colony-specific foraging areas. Ecol Monogr 74:159–178. https://doi.org/10.1890/02-4073

Ainley DG, Dugger KM, Mesa ML et al (2018) Post-fledging survival of Adélie penguins at multiple colonies: chicks raised on fish do well. Mar Ecol Prog Ser 601:239–251. https://doi.org/10.3354/meps12687

Alexander RD (1974) The evolution of social behavior. Annu Rev Ecol Syst 5:325–383. https://doi.org/10.1146/annurev.es.05.110174.001545

Ashmole NP (1963) The regulation of numbers of tropical oceanic birds. Ibis 103b:458–473. https://doi.org/10.1111/j.1474-919X.1963.tb06766.x

Ballance LT, Ainley DG, Ballard G, Barton K (2009) An energetic correlate between colony size and foraging effort in seabirds, an example of the Adélie penguin *Pygoscelis adeliae*. J Avian Biol 40:279–288. https://doi.org/10.1111/j.1600-048X.2008.04538.x

Birt VL, Birt TP, Goulet D et al (1987) Ashmole's halo: direct evidence for prey depletion by a seabird. Mar Ecol Prog Ser 40:205–208

Black C, Collen B, Johnston D, Hart T (2016) Why huddle? Ecological drivers of chick aggregations in Gentoo penguins, *Pygoscelis papua*, across latitudes. PLoS ONE 11:e0145676. https://doi.org/10.1371/journal.pone.0145676

Blus LJ, Keahey JA (1978) Variation in reproductivity with age in the brown pelican. Auk 95:128–134. https://doi.org/10.2307/4085503

Boulinier T, Danchin E, Monnat J-Y et al (1996) Timing of prospecting and the value of information in a colonial breeding bird. J Avian Biol 27:252–256. https://doi.org/10.2307/3677230

Brown CR (2016) The ecology and evolution of colony-size variation. Behav Ecol Sociobiol 70:1613–1632. https://doi.org/10.1007/s00265-016-2196-x

Burger J (1978) Competition between cattle egrets and native North American herons, egrets, and ibises. The Condor 80:15–23. https://doi.org/10.2307/1367786

Carrascal LM, Moreno J, Amat JA (1995) Nest maintenance and stone theft in the chinstrap penguin (*Pygoscelis antarctica*). Polar Biol 15:541–545. https://doi.org/10.1007/BF00239645

Chapman EW, Hofmann EE, Patterson DL et al (2011) Marine and terrestrial factors affecting Adélie penguin *Pygoscelis adeliae* chick growth and recruitment off the western Antarctic Peninsula. Mar Ecol Prog Ser 436:273–289. https://doi.org/10.3354/meps09242

Cook TR, Gubiani R, Ryan PG, Muzaffar SB (2017) Group foraging in Socotra cormorants: a biologging approach to the study of a complex behavior. Ecol Evol 7:2025–2038. https://doi.org/10.1002/ece3.2750

Coulson J (2002) Colonial breeding in seabirds. Biology of marine birds. CRC Press, Boca Raton, pp 87–113

Coulson JC, White E (1958) The effect of age on the breeding biology of the kitttwake *Rissa tridactyla*. Ibis 100:40–51. https://doi.org/10.1111/j.1474-919X.1958.tb00364.x

Cox A, Schmidt A (2023) Pointblue/solo_nests: v1.0.1. https://doi.org/10.5281/zenodo.8284755

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

Davis LS (1982) Creching behaviour of Adélie penguin chicks (*Pygoscelis adeliae*). NZ J Zool 9:279–285. https://doi.org/10.1080/03014223.1982.10423856

Dowle M, Srinivasan A (2023) data.table: Extension of `data.frame`

Dugger KM, Ballard G, Ainley DG et al (2014) Adélie penguins coping with environmental change: results from a natural experiment at the edge of their breeding range. Front Ecol Evol. https://doi.org/10.3389/fevo.2014.00068

Emslie SD, Coats L, Licht K (2007) A 45,000 yr record of Adélie penguins and climate change in the Ross Sea, Antarctica. Geology 35:61–64. https://doi.org/10.1130/G23011A.1

Forbes LS, Kaiser GW (1994) Habitat choice in breeding seabirds: when to cross the information barrier. Oikos 70:377–384. https://doi.org/10.2307/3545775

Forbes LS, Jajam M, Kaiser GW (2000) Habitat constraints and spatial bias in seabird colony distributions. Ecography 23:575–578

Fox J, Weisberg S (2019) An R companion to applied regression, 3rd edn. SAGE, Los Angeles

Furness RW, Birkhead TR (1984) Seabird colony distributions suggest competition for food supplies during the breeding season. Nature 311:655–656. https://doi.org/10.1038/311655a0

Gilbert C, Robertson G, Le Maho Y et al (2006) Huddling behavior in emperor penguins: dynamics of huddling. Physiol Behav 88:479–488. https://doi.org/10.1016/j.physbeh.2006.04.024

Grolemund G, Wickham H (2011) Dates and times made easy with lubridate. J Stat Soft. https://doi.org/10.18637/jss.v040.i03

Hamilton WD (1971) Geometry for the selfish herd. J Theor Biol 31:295–311. https://doi.org/10.1016/0022-5193(71)90189-5

Hinke JT, Giuseffi LM, Hermanson VR et al (2022) Evaluating thermal and color sensors for automating detection of penguins and pinnipeds in images collected with an unoccupied aerial system. Drones 6:255. https://doi.org/10.3390/drones6090255

Jennings S, Varsani A, Dugger KM et al (2016) Sex-based differences in Adélie penguin (*Pygoscelis adeliae*) chick growth rates and diet. PLoS ONE 11:e0149090. https://doi.org/10.1371/journal.pone.0149090

Jennings S, Dugger KM, Ballard G, Ainley DG (2021) Effects of diet and provisioning behavior on chick growth in Adélie penguins (*Pygoscelis adeliae*). Cowa 44:55–67. https://doi.org/10.1675/063.044.0105

Jennings S, Dugger KM, Ballard G, Ainley DG (2023) Faster growth and larger size at crèche onset are associated with higher offspring survival in Adélie penguins. Ornithology. https://doi.org/10.1093/ornithology/ukad006

Kassambara A (2023) ggpubr: "ggplot2" based publication ready plots

Kildaw SD (1999) Competitive displacement? An experimental assessment of nest site preferences of cliff-nesting gulls. Ecology 80:576–586. https://doi.org/10.2307/176636

Lack D (1967) Interrelationships in breeding adaptations as shown by marine birds. In: Proceedings of the International Ornithological Congress. Blackwell Scientific Publications Oxford, Oxford, pp 3–42

LaRue MA, Ainley DG, Swanson M et al (2013) Climate change winners: receding ice fields facilitate colony expansion and altered dynamics in an Adélie penguin metapopulation. PLoS ONE 8:e60568. https://doi.org/10.1371/journal.pone.0060568

Larue M, Iles D, Labrousse S et al (2019) A possible Adélie penguin sub-colony on fast ice by Cape Crozier, Antarctica. Antarct Sci 31:189–194. https://doi.org/10.1017/S095410201900018X

Lescroël A, Dugger KM, Ballard G, Ainley DG (2009) Effects of individual quality, reproductive success and environmental variability on survival of a long-lived seabird. J Anim Ecol 78:798–806. https://doi.org/10.1111/j.1365-2656.2009.01542.x

Long JA (2022) jtools: Analysis and presentation of social scientific data

Lynch HJ, LaRue MA (2014) First global census of the Adélie penguin. Auk 131:457–466. https://doi.org/10.1642/AUK-14-31.1

Lyver PO, Barron M, Barton KJ et al (2014) Trends in the breeding population of Adélie penguins in the Ross Sea, 1981–2012: a coincidence of climate and resource extraction effects. PLoS ONE 9:e91188. https://doi.org/10.1371/journal.pone.0091188

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

Nisbet ICT (1975) Selective effects of predation in a tern colony. The Condor 77:221–226. https://doi.org/10.2307/1365803

Patterson IJ (1965) Timing and spacing of broods in the black-headed gull *Larus ridibundus*. Ibis 107:433–459. https://doi.org/10.1111/j.1474-919X.1965.tb07330.x

Penney RL (1968) Territorial and social behavior in the Adélie penguin. In: Antarctic Bird Studies. American Geophysical Union (AGU), pp 83–131

R Core Team (2022) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria

Santora JA, LaRue MA, Ainley DG (2020) Geographic structuring of Antarctic penguin populations. Glob Ecol Biogeogr 29:1716–1728. https://doi.org/10.1111/geb.13144

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 11:15380. https://doi.org/10.1038/s41598-021-94861-7

Sladen WJL (1958) The Pygoscelid penguins: I. Methods of study. II. The Adélie penguin. HMSO, London

Stonehouse B (1962) The tropic birds (genusphaethon) of Ascension Island. Ibis 103B:124–161. https://doi.org/10.1111/j.1474-919X.1962.tb07242.x

Taylor RH (1962) The Adelie penguin *Pygoscelis adeliae* at Cape Royds. Ibis 104:176–204. https://doi.org/10.1111/j.1474-919X.1962.tb08644.x

Tenaza R (1971) Behavior and nesting success relative to nest location in Adélie penguins (*Pygoscelis adeliae*). The Condor 73:81–92. https://doi.org/10.2307/1366127

Tims J, Nisbet ICT, Friar MS et al (2004) Characteristics and performance of common terns in old and newly-established colonies. Cowa 27:321–332. https://doi.org/10.1675/1524-4695(2004)027[0321:CAPOCT]2.0.CO;2

Treisman M (1975) Predation and the evolution of gregariousness. I. Models for concealment and evasion. Anim Behav 23:779–800. https://doi.org/10.1016/0003-3472(75)90106-2

Venables WN, Ripley BD (2002) Modern applied statistics with s, fourth. Springer, New York

Wethington M, Flynn C, Borowicz A, Lynch HJ (2023) Adélie penguins north and east of the 'Adélie gap' continue to thrive in the face of dramatic declines elsewhere in the Antarctic Peninsula region. Sci Rep 13:2525. https://doi.org/10.1038/s41598-023-29465-4

Wickham H, Averick M, Bryan J et al (2019) Welcome to the tidyverse. JOSS 4:1686. https://doi.org/10.21105/joss.01686

Wickham H, Bryan J (2023) readxl: Read excel files

Wilcoxon F (1945) Individual comparisons by ranking methods. Biom Bullet 1:80. https://doi.org/10.2307/3001968

Wilke CO (2020) cowplot: Streamlined plot theme and plot annotations for "ggplot2"

Williams AJ (1975) Guillemot fledging and predation on Bear Island. Ornis Scandinavica (scand J Ornithol) 6:117–124. https://doi.org/10.2307/3676225

Wittenberger JF, Hunt GL (1985) The adaptive significance of coloniality in birds. Avian Biology. Elsevier, Amsterdam, pp 1–78

Young E (1994) Skua and penguin: predator and prey. Cambridge University Press, Cambridge