



Maintenance of nest quality in Adélie penguins *Pygoscelis adeliae*: an additional benefit to life in the center

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Abstract

In colonial seabirds, differences in the nesting or fledging success have been associated with differences in nest position within the breeding aggregation (subcolony): less successful nests are located on the periphery, with more successful nests closer to the center. For *Pygoscelid* penguins, central nests tend to be larger, with nest size being an indicator of individual quality because stones must be gathered singly, so more stones reflect more individual effort. Competition for nest materials, including the collection of materials from another's nest, has also frequently been described in penguins and other colonial seabirds. We used the data collected during the incubation stage from a total of 20 subcolonies at two separate breeding colonies of Adélie penguins (*Pygoscelis adeliae*) on Ross Island (Antarctica) to test the influence of nest position on breeding success. We also investigated how competition for nest stones could occur at different intensities depending on size of the subcolony, nest position, and quality within a subcolony. We found that peripheral nests experienced lower breeding success and higher number of individuals attempting to remove stones with higher removal success rates than from nests toward the center. The higher costs associated with maintaining and defending nests that incur higher removal pressure could be an additional factor involved in the lower breeding success of peripheral nests.

Keywords Breeding sites · Habitat heterogeneity hypothesis · Nest quality · Coloniality · Adélie penguin · Antarctica · Stones

Introduction

Competition for breeding sites is well described in birds (Ferrer and Donazar 1996; Newton 1998; Kokko et al. 2004), with several examples of site-dependent fecundity documented for territorial (Dhondt and Kempenaers 1992; Ferrer and Donazar 1996; Krüger et al. 2012; Morandini et al. 2017) and colonial–nesting species (Ainley 2002; Kokko et al. 2004; Ferrer et al. 2014). One of the most useful models for explaining individual settlement patterns among

territorial species is the ideal despotic model (Fretwell and Lucas 1969), in which the best quality individuals (older/more experienced or dominant), and/or the first to arrive (best body condition), monopolize the highest quality sites (Sergio and Newton 2003). Thus, territorial behavior prevents access to these high-quality sites by lower quality (younger/less experienced or subordinate) and/or later arriving individuals, who are then relegated to progressively inferior territories (Fretwell and Lucas 1969; Sergio and Newton 2003).

In colonial seabirds, differences in the nesting or fledging success have been associated with differences in nest position within the breeding aggregation (subcolony), with less successful nests on the edge and more successful nests closer to the center (Penney 1968; Ainley et al. 1983; Barbosa et al. 1997; Ainley 2002; Vergara and Aguirre 2006; Liljesthrom et al. 2008). Differences in success of peripheral vs. central nests have been associated with a variety of factors including (1) age and/or breeding experience of breeding birds (with younger and/or less experienced birds occupying peripheral positions; Spurr 1975; Ainley et al.

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1983; see also Barbosa et al. 1997; Vergara and Aguirre 2006), (2) predation rates (decreasing from peripheral nests toward central positions; Brown and Brown 2001), (3) protection from adverse weather conditions (more protection in central positions; Ferrer et al. 2014), and (4) the extent of interactions among individuals (with peripheral positions more likely to be disturbed than central nests; Kokko et al. 2004; Ferrer et al. 2014).

It has also been reported for *Pygoscelid* penguins that central nests tend to be larger (e.g., more stones; e.g. Fargallo et al. 2001), with nest size being an indicator of individual quality because stones must be gathered singly, so more stones reflect more individual effort (Ainley et al. 1983; Fargallo et al. 2004). However, time and energy spent on building nests must be balanced with other reproductive activities (Stearns 1992; Fargallo et al. 2001) and competition for nest materials, including taking of materials from another's nest, has frequently been described in seabirds (Carrascal et al. 1995; Fargallo et al. 2001; Ainley 2002). The potential advantages of taking nest material from another's nest include (1) increased rate of material acquisition (Cullen 1957; Burger 1974; Schleicher et al. 1993), (2) reduced energy costs compared to traveling a greater distance outside the colony (Collias and Collias 1978; Wittenberger and Hunt 1985), (3) reduced time/energy costs as compared to collecting material in an unfamiliar area (Cullen 1957), and (4) acquisition of higher quality materials (Burger 1974). Usually, in *Pygoscelis* penguins, both mates are involved in nest building and carry stones in their beaks to prepare or maintain a layer of stones added to a scoop in the ground forming a bowl for the nest (Ainley et al. 1983; Müller-Schwarze 1984). During the incubation and brooding stages of nesting, mates alternate shifts of incubating eggs, brooding, guarding chicks, and foraging at sea. Upon the return of a mate, the bird recently relieved from incubation/brooding/guarding duties typically collects stones for its nest from the surrounding area, including taking stones from other birds' nests (Carrascal et al. 1995; Hunter and Davis 1998; Fargallo et al. 2001). Nest-maintenance activity is primarily thought to have evolved in some penguin species to improve thermal nest characteristics, contributing toward improving offspring survival (Tenaza 1971; Carrascal et al. 1995; Fargallo et al. 2001). Thus, nest size represents an important property of the nest as bigger nests (i.e., nests with more stones) are less likely to be flooded by melt water (Levick 1914; Tenaza 1971; Moreno et al. 1995, 1999), and stone-collecting behavior may strengthen pair bonds (Roberts 1940). Stone gathering also constitutes a displacement activity in agonistic situations, developing further into a behavior signal of nest ownership (Ainley 1974, 1975). Finally, when evaluating questions about nest quality relative to location within subcolonies, it is important to consider subcolony size, because the previous work with

chinstrap penguins (*Pygoscelis antarctica*) reported marked differences between large and small subcolonies in nest size, stone availability, and other aspects of breeding ecology and nesting success (Carrascal et al. 1995; De Neve et al. 2006). In addition, as subcolonies increase in size, more penguins pass through edge nests increasing the unfavorable effects of these interactions (Ferrer et al. 2014), but subcolonies shape will affect the relationship between subcolony size (total number of nests) and the rate of edge nests per total nests.

In this study, we investigated how competition for nest stones could occur at different intensities relative to nest position within subcolonies of Adélie penguins (*Pygoscelis adeliae*). Previous studies showed that stone-provisioning behavior is a nest-maintenance activity evolved to improve thermal nest characteristics potentially increasing offspring survival, and competing in time and energy with other reproductive activities (Fargallo et al. 2001), with differences between sexes (Moreno et al. 1995) and dependent on stone accessibility (Carrascal et al. 1995). We evaluated differences in the stone collecting behavior of penguins at different nest positions within a subcolony, hypothesizing that nest maintenance behavior, in addition to other factors (e.g., heat loss; Ferrer et al. 2014), reflected nest site quality, and could in part, explain differences in breeding success between peripheral and central nests. We predicted that a higher number of birds attempt to take stones from nests located at the edges of the subcolonies, the lower quality sites experiencing lower breeding success. Moreover, differences in the size of subcolonies with primarily circular configurations may affect the number of birds attempting to take stones on peripheral and central nests, due to the relative proportion of peripheral vs. central nests.

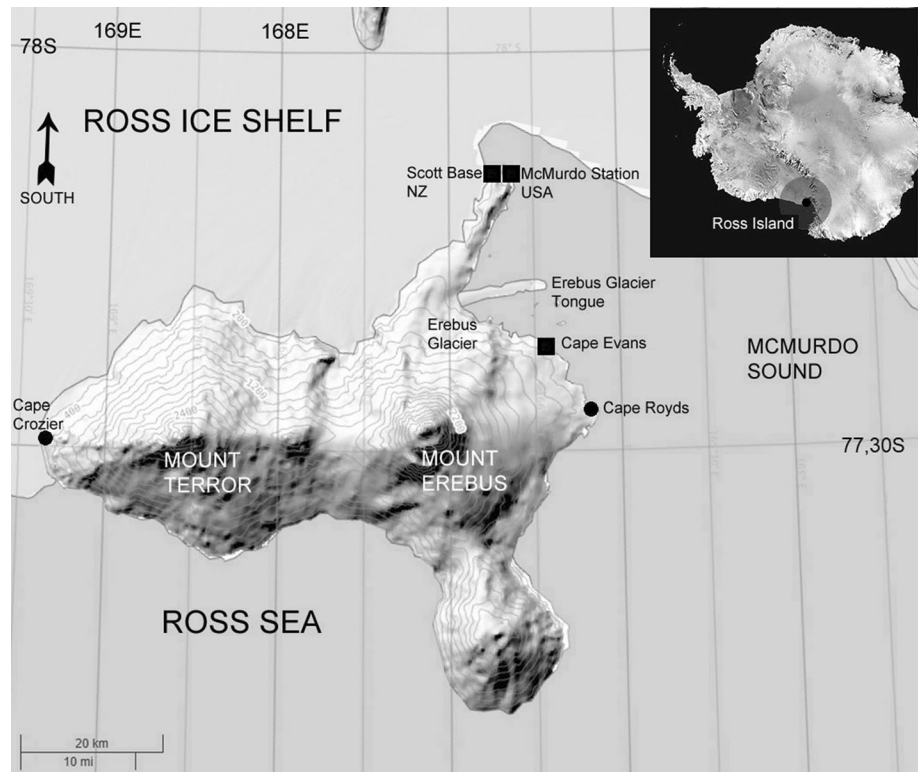
Methods

Data collection

Approximately 33–38% of the world's Adélie penguin population breed in the Ross Sea, and the four colonies of the southwestern Ross Sea metapopulation (~10% of world population) represent the southernmost breeding range for the species (Lynch and LaRue 2014; Lyver et al. 2014). Our study was carried out at two different colonies located on Ross Island in the Ross Sea: Cape Royds (~3000 breeding pairs) and Cape Crozier (~300,000 breeding pairs; Lyver et al. 2014)(Fig. 1).

First, we recorded breeding success relative to nest location from different subcolonies at the Cape Crozier colony during the 2017–2018 breeding season. We located nests of 400 birds banded with flipper bands and with a breeding history recorded over the years, by searching the colony weekly from the onset of egg laying in late October, through

Fig. 1 Map of Ross Island showing the location of Cape Royds and Cape Crozier. Source “SCAR Antarctic Digital Database”



creching in mid-January. We recorded breeding success (1 = successful nest if at least one chick entered in crèche and 0 = failed nest if no chicks crèched), and nest position (“1” = a nest on the outside edge, with position number increasing to the center of the subcolony) for each known breeding bird. Nest position can vary depending the time of the season (as some nests might fail and be abandoned) and the observer (potential differences in the ability to count nest position). To account for this, we selected the nest position that was most repeated among different observers from the beginning of the incubation period (2nd Nov; first egg seen) until the first crèche was seen (26th Dec) among all the observations recorded during the season. If different positions were recorded the same number of times for a particular nest, the position closest to the edge of the subcolony was selected and we only included nests where nest position was recorded ≥ 2 times before creching.

We included observations from both Cape Royds and Cape Crozier colonies to investigate whether nest maintenance behavior related to nest position. We collected behavioral data during the incubation stage of the reproductive cycle (1–18 December 2017), from 13 subcolonies at Cape Royds, and 7 subcolonies at Cape Crozier. We randomly selected subcolonies and conducted observations for approximately 30 min at a distance that did not affect the penguins’ behavior (≥ 5 m). However, we excluded long, linear colonies with less than seven nest positions between the edge and the center of the colony from this analysis because there are

essentially no center nests in subcolonies with this configuration. Owing to differences in subcolony size, we sampled some subcolonies more than once, moving the observation area every 30 min to avoid observations on the same nests. We recorded all attempts by the birds to take stones from another nest during this 30 min observation time at each visit in each subcolony. However, as penguins tended to take stones repeatedly from the same nests during a bout of stone gathering, we only recorded the first attempt for the same nest for a given individual. We defined a “source” nest as a nest where we observed an individual attempting to take a stone. We defined a “home” nest as the original nest belonging to the individual observed taking a stone, which we identified by following the bird back to its own nest with the stone. If the home nest was not clearly identified (due to the ambiguous behavior of the bird, or difficulty-tracking individuals within a subcolony) we only recorded the source nest.

Each time a bird attempted to remove a stone from a nest, we recorded information about the nest from which the stone was taken (source nest), and when the bird was successfully tracked back to its own nest, the home nest. We recorded (1) nest position (i.e., number of nests that occurred between the nest in question and the subcolony outside edge; “1” = a nest on the outside edge, with position number increasing to the center of the subcolony); (2) nest quality, and (3) nest attendance (attended vs unattended, depending on whether the owner of the nest was

present). We characterized nest quality relative to the layer of stones covering the base of the nests. A minimum layer of stones covering the entire base of the nests was required to insulate the nest contents from the ground and protect them from melt water as ambient temperatures increased during incubation. The diameter of the stones used in building the nests is ~ 2 cm, and nests with less than 2 cm of stones cover over the base of the nest put nest contents in contact with the bare ground. We categorized these nests as “poorly built”. In contrast, we categorized nests with stones completely covering the bottom of the nest at a depth of ≥ 2 cm as “well-built” nests. We always characterized nests based on the observations by the same person by direct observation of the base of the nest. If an incubating bird was occupying the nest, nest quality was characterized without altering the normal behavior of the sitting bird, waiting until the bird changed position or moved to defend its own nest from an intruder. We also classified each stone removal attempt as either successful (if the bird removing the stone was able to take a stone from the source nest), or unsuccessful (if the owner of the source nest prevented stone removal by engaging in aggressive behavior, e.g., threat, pecking, or hitting it with rapid flipper strokes).

We estimated subcolony size by counting all the nests in the subcolony (conducted by one person) and we binned size into one of two categories reflecting the distribution of the subcolony sizes sampled: small (< 300 breeding pairs) vs. large (> 300 breeding pairs) (Fig. 2).

Statistical analyses

We used a point–biserial correlation, a special case of the product–moment correlation in which one variable is continuous and the other variable is binary to investigate the correlation between breeding success as binomial variable (0 = failed nest; 1 = successful nest) and nest position as continuous variable (from nest position 1 to nest position 10). In addition, we also developed two a priori model sets and used mixed effect logistic models with binomial error distribution, and logit link to test our nest maintenance hypotheses. We developed the first model set to evaluate differences in nest characteristics between “source” (nests subjected to stone removal) and “home” nest (nests belonging to the bird who has taken the stone) with “home” nests as the reference (i.e., home = 0). We included all home and source nests recorded during our study period in this analysis, and our model set included five models with various combinations of the variables “nest position” and “subcolony size” (see Table 1). We tested differences in the proportion of peripheral nests vs. central nests in big and small subcolonies, by investigating the interaction between “nest position” and “subcolony size” (Table 1).

We developed a second model set to investigate factors associated with the probability of successfully removing a stone from an attended source nest (failure = 0, success = 1). In this model, we focused on attended nests only, because without any birds to dissuade potential intruders, there was no barrier to successful stone removal (i.e., stone removal success = 100%). Therefore, for the second analysis, we included only observations from attended source nests. In this model,

Fig. 2 Distribution of the observations of “stone removal events” in the different subcolony sizes sampled at Cape Crozier, Ross Sea, during the breeding season 2017/18

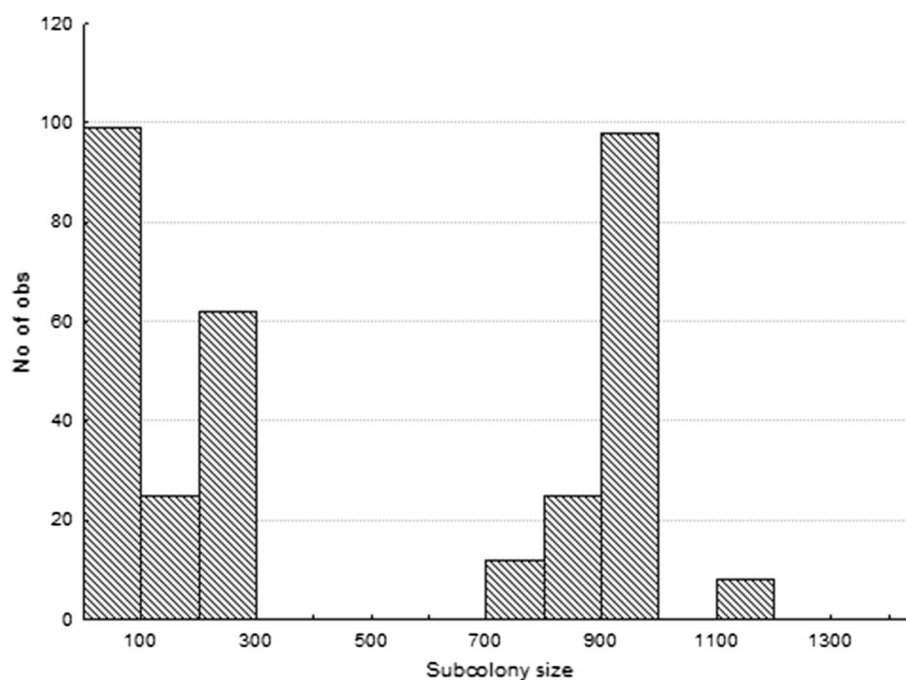


Table 1 The results from mixed effect logistic models (using a binomial distribution with logit link) from two model sets used to evaluate (A) the probability that a nest was the “source” of stones collected by another bird for their own nest and (B) the probability that an individual was successful taking a stone from an attended source nest

Model	AIC _c	ΔAIC _c	K	w _i	Log likelihood
1. Probability of being a “source” nest (<i>n</i> = 329)					
NP + SS + NP*SS	385.018	0.000	5	0.746	− 187.41
NP + SS	387.964	2.946	4	0.171	− 189.92
NP	389.422	4.404	3	0.083	− 207.15
Intercept only	419.197	34.179	2	0.000	− 191.67
SS	420.370	35.351	3	0.000	− 207.58
2. Probability of successfully removing a stone from an attended source nest (<i>n</i> = 128)					
NP	167.666	0.000	3	0.702	− 80.736
NP + SS	169.467	1.800	4	0.285	− 80.571
Intercept only	176.223	8.557	2	0.010	− 86.064
SS	178.287	10.621	3	0.003	− 86.047

Both models included subcolony as a random effect

NP = nest position; SS = subcolony size

*Model 1: source nest = 1; target nest = 0. Model 2: success removing a stone = 1; failure = 0

we did not explore the interaction between “nest position” and “subcolony” size, because excluding unattended source nests reduced the sample size available for analysis.

For both analyses, if covariates included in the models were correlated with $r > 0.70$ with a point-biserial correlation we did not include both parameters in the same model. We did include subcolony as a random effect in all models to account for any within-subcolony variation associated with multiple observations at each subcolony. We used an information-theoretic approach to develop a priori model sets and we ranked models using Akaike’s information criterion corrected for small sample sizes (AIC_c), ΔAIC_c (the difference in AIC_c between each candidate model and the model with the lowest AIC_c value), and Akaike weights (AIC_c weights; Burnham and Anderson 2002). Models within 2 ΔAIC_c values of the top model were considered competitive. The degree to which 95% confidence intervals for slope coefficients (β) overlapped zero was also used to evaluate the strength of evidence for competing models within the model set (Arnold 2010; Dugger et al. 2016). We used the ‘lme4’ package (Bates et al. 2014) in R Version 1.1.423 (R Development Core Team 2013) to general model coefficients and model selection statistics.

Results

For the 400 attended nests we evaluated at Cape Crozier, nests towards the center of a subcolony had higher breeding success than nests located in peripheral position (Point biserial

correlation = 0.149; $t = 2.9904$, $df = 395$, $p = 0.002961$; 95% CI: 0.051–0.244). We recorded 329 stone removal events ($n = 208$ source nests; $n = 121$ target nests) for both Cape Crozier and Cape Royds colonies at 20 different subcolonies, ranging in size from 46 to 1189 nests (Fig. 2). We recorded nest position ranging from 1 (nests at the edge) to 7, and nest quality (1 = well-built nests; 2 = poorly built nests) was significantly correlated with nest position (point biserial correlation = − 0.264, $t = -4.857$, $p < 0.001$), indicating that peripheral nests were lower quality as compared to those farther away from the edge.

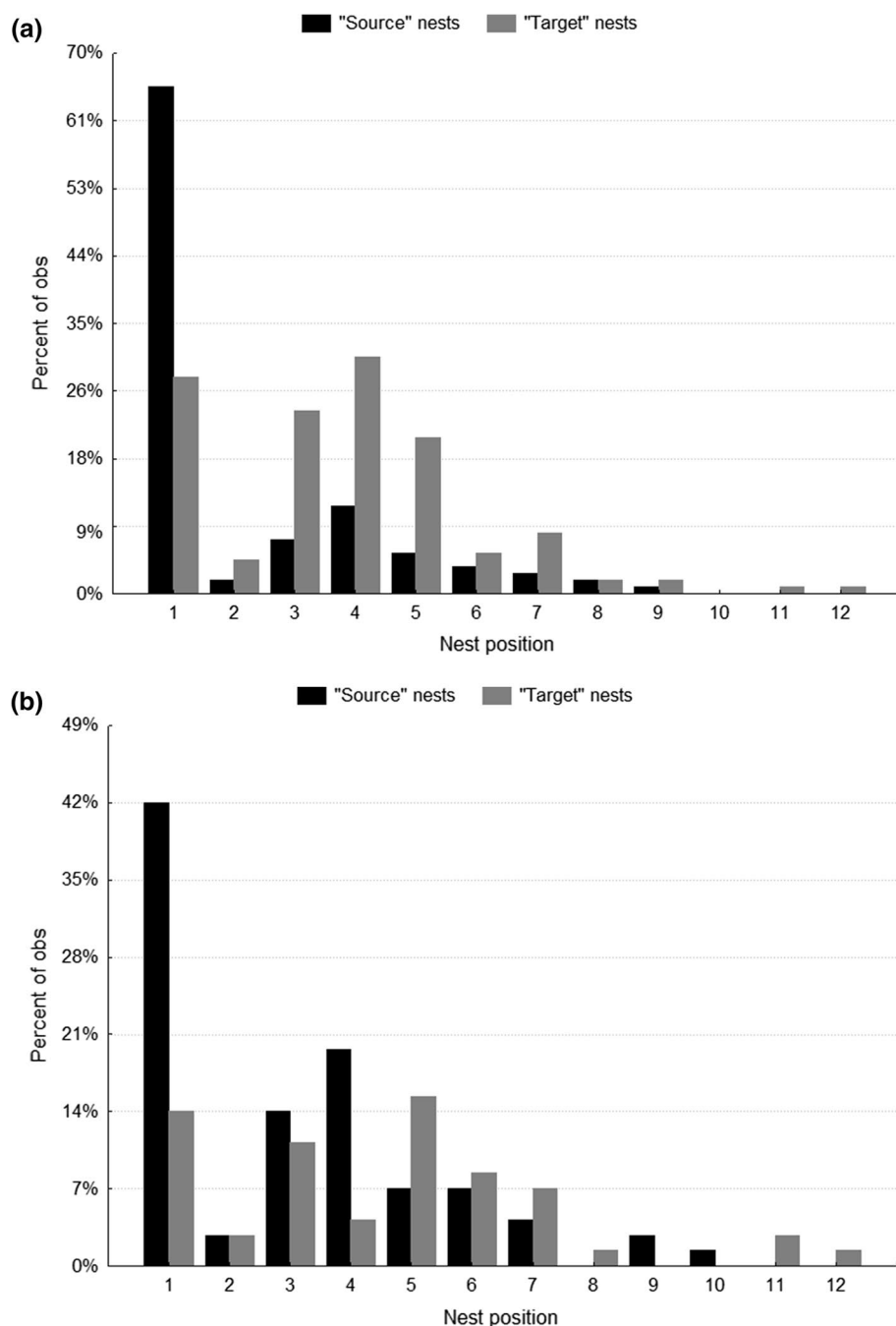
The model relating the probability of becoming a source nest with an interaction between nest position and subcolony size received the most support (74% of the AIC_c weight). The main effects indicated that nests closer to the edge had a higher probability of becoming source nests ($\hat{\beta}_{\text{nest position}} = -0.825$, $SE = 0.219$, 95% CI’s: − 1.255 to − 0.395), and the probability of being a source nest was higher in larger subcolonies, although this main effect was weaker as 95% CIs broadly overlapped zero ($\hat{\beta}_{\text{subcolony size}} = -0.129$, $SE = 0.438$; 95% CI’s: − 0.987 to 0.729). However, the interaction between nest location and subcolony size was very important, and suggested that the probability of being a source nest declined more rapidly as nest location moved towards the center in small as compared to large subcolonies ($\hat{\beta}_{\text{nest position} \times \text{subcolony size}} = 0.304$, $SE = 0.137$; 95% CIs: 0.036–0.573) (Fig. 3 and Fig. 4). Considering only “source” nests that were attended, the variables “nest position” and “nest quality” were again significantly correlated ($n = 134$; point biserial correlation = − 0.339, $t = -4.138$, $p < 0.001$), with peripheral nests being of lower quality than nonperipheral nests.

The probability of successfully removing a stone from an attended nest was most strongly associated with nest position (Table 1; $\hat{\beta} = -0.332$, $SE = 0.108$; 95% CI’s: − 0.543 to − 0.120) and individuals were more successful removing stones from peripheral “source nests” than from nests located progressively toward the subcolony center as predicted (Fig. 5). A second model was competitive (ΔAIC_c ≤ 2.0) and this model contained nest position as well as subcolony size (Table 1). However, the best model containing only nest position had more than twice the support than the 2nd best model. In addition, the 95% CIs on the “subcolony size” model coefficient broadly overlapped zero ($\hat{\beta} = 0.219$, $SE = 0.382$; 95% CI’s: − 0.529 to 0.968) indicating little support for this effect (Arnold et al. 2010; Dugger et al. 2016).

Discussion

Preferences for high-quality habitats or territories appear extremely widespread in birds (Ainley et al. 1983; Sergio and Newton 2003; Kokko et al. 2004; Krüger et al. 2012;

Fig. 3 Frequencies of observations of “source” and “target” nests recorded in both **A** “small” and **B** “big” subcolonies at Cape Royds and Cape Crozier, Ross Sea, in 2017



Morandini et al. 2017). In most seabird colonies, nests are distributed along a periphery- to- center gradient, and high-quality nests are found closer to the center of the distribution (Barbosa et al. 1997; Minguez et al. 2001; Ferrer et al. 2014). Consistent with these previous finding, we found that nests exhibiting higher breeding success were located closer to the subcolony interior rather than the outer edge. Previous Adélie penguin’s studies (Ainley 1983, 2002) showed that more experienced Adélie penguins nest 1–2 nests in from the edge rather than at very central positions, even that, our data show that the

probability of being a “source” nest decreases toward central positions.

Because the frequency of interactions among penguins can shift from the center to the edge of the subcolony, peripheral nesters are more likely to be disturbed (up to eight times more) than central nesters (Ferrer et al. 2014). Exposure to a higher number of interactions with neighbors and individuals crossing peripheral limits of subcolonies to access central nests in our study may explain why nests located closer to the edge of subcolonies had a higher probability of being source nests for stone-gathering penguins

Fig. 4 The predicted probability and 95% confidence intervals (shaded area) that a nest becomes a “source” nest from our best mixed effects logistic regression model including the interaction between nest position and subcolony size and subcolony as a random effect for Adélie penguins at capes Royds and Crozier, on Ross Island, Antarctica during 2017–2018 breeding season. Predicted probabilities for nests in “big” colonies (> 300 breeding pairs) are represented in blue and those for nests in “small” colonies (< 300 breeding pairs) in red

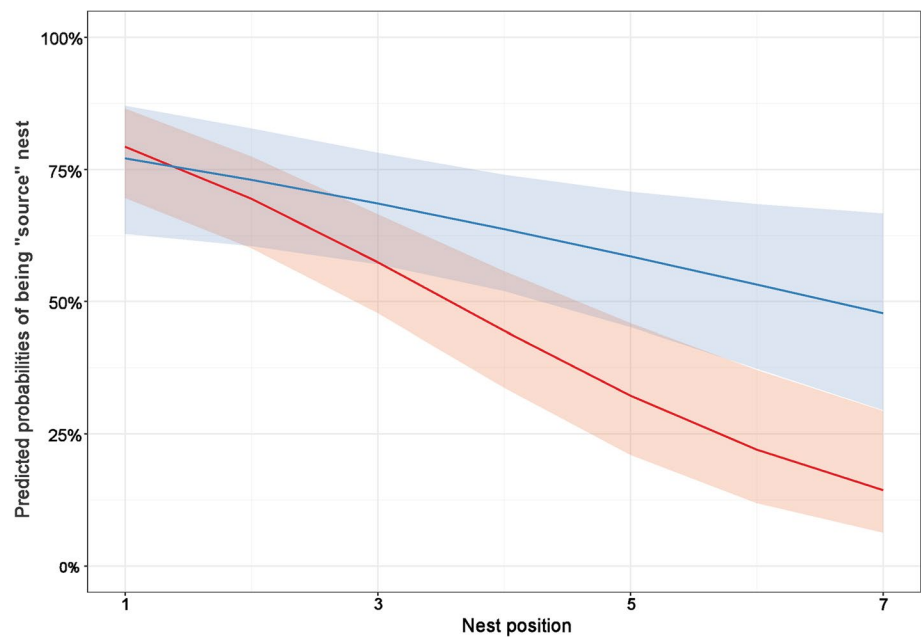
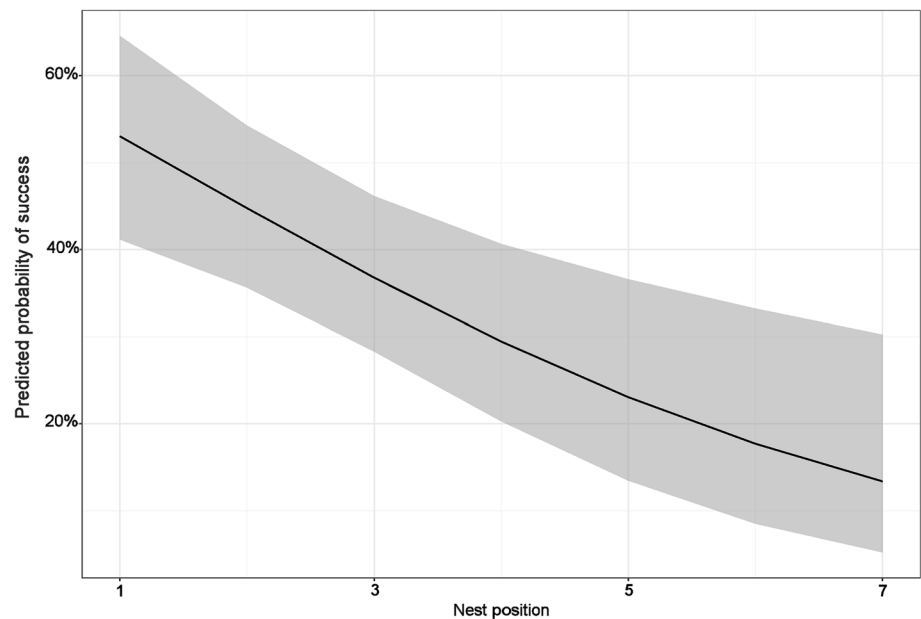


Fig. 5 The predicted probability of success and 95% confidence intervals (shaded area) when taking a stone from a source nest from our best-mixed effects logistic regression model including the nest position in the subcolony for Adélie penguins at capes Royds and Crozier, Ross Island, Antarctica, during 2017–2018 breeding season



and why nest quality increased with central position. In this sense, peripheral nests are subjected to a higher frequency of intrusions by individuals attempting to take stones than nests located in more central positions. Individuals continuously monitor the size of their own nest throughout the incubation–brooding period, reacting to changes in nest size by appropriate changes in stone-collecting rate (Moreno et al. 1999). Thus, the nest’s owners maintain the quality of attended nests by stone collecting throughout incubation with consequent energy costs. Nests in central positions in the subcolonies at Cape Crozier and Cape Royds during the breeding season 2017/18 were bigger and were “source”

nests less often than those located at the edge of the colonies. Given these results, we might predict that peripheral nest owners would expend more energy in nest maintenance than those with more central nests. However, in our study, we cannot separate individual quality and nest position, higher nest quality, and breeding success could be a consequence of higher individual quality inside a subcolony and differences in personality. In this case, a higher stone removal attempts and the higher success would reflect the personality of birds nesting at peripheral positions. Future studies should attempt to separate the importance of nest position, and individual quality and personality through field experiments.

Subcolony size may be an important component of nest location and subsequent nest quality, because the number of nests may be associated with the availability of nest materials in the area surrounding the subcolony, affecting both the frequency of stone removal attempts and the quality of nests (Carrascal et al. 1995). The interaction we observed between nest position and subcolony size on the probability that a nest is a “source” nest could reflect the effect of the typical shape configuration of Adélie penguin subcolonies, we sampled in our study. In round or oval shaped subcolonies, an increase in subcolony size results in more “central” relative to “peripheral” nests, so disproportionately more penguins must pass through peripheral nests to get to central nests increasing the stones removal attempts at peripheral nest located in bigger subcolonies. This increases the potential for interactions among individuals in nests closer to peripheral positions (Ferrer et al. 2014). Thus, nests located closer to the subcolony edge are disturbed more frequently and it becomes easier to successfully remove stones from these nests.

Our results show that nest quality increases with nest position and individuals tend to attempt to remove stones more often from nests closer to the edge than from nests toward the center, with higher removal success rates occurring in these peripheral nests. It is likely that the presence of neighbors increases the general vigilance around territorial intrusions, and this could deter birds attempting to remove stones. The level of aggression towards intruders by individuals nesting in central sites is higher than by birds at colony edges (a difference that could be due to the lower residual reproductive value of central-nesting, probably older birds; Viñuela et al. 1995). Indeed, we recorded attacks from all the neighbors on birds trying to remove stones from central source nests, in addition to attacks from birds of source nests (VM pers. obs.). Higher levels of aggressions toward intruders (Viñuela et al. 1995) and attacks from neighbors may help reduce intruders from targeting more central nests. Interestingly, despite the better quality of central nests (i.e., they contain more stones), factors most associated with the higher number of source nests on the subcolony periphery included the lower success preventing stones removal from their own nests by birds from peripheral nests, the lack of additional defense from neighbors, and the higher aggressiveness of individuals from central positions. Thus, selecting nests located in central positions within subcolonies may confer an advantage, as pressure from individuals trying to remove stones is reduced as compared to nests closer to the subcolony edge.

Our results show that central nests are bigger, have a lower probability of being a source nest for stone removal activities, and a higher probability of being successful, compared to nests on the subcolony periphery. Predation of eggs and chicks by South Polar skuas (*Stercorarius maccormicki*)

is an important factor that drives Adélie penguin numbers and the lower breeding success observed in peripheral nests (Ainley 2002; Wilson et al. 2017), and the amelioration of climate effects is an additional factor that drives differences in productivity between peripheral and central nests (Ferrer et al. 2014). Our results show that in addition to those factors benefitting central nests, central nests appear to experience less disturbance related to stone removal by neighbors. Thus, subcolony configuration and the ratio of central to peripheral nests within the colony show differences in the stealing-stones pressure that agree with population-level reproductive success, highlighting the stealing-stone pressure as one potential factor affecting reproductive success in *Pygoscelis* penguins.

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Author contributions VM conceived and designed research. All authors conducted fieldwork. KMD and VM analyzed data. All authors wrote the manuscript, and read and approved the manuscript.

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Declarations

Conflict of interest Authors declare that there are not any conflicts of interest or competing interest.

Ethical approval Fieldwork was conducted under Antarctic Conservation Act permit ACA 2017-005, and Assurance of Compliance with NSF Requirements on Humane Care and Use of Vertebrate Animals—NSF proposal 1543498 and 1543459. Permits were provided under the Antarctic Conservation Act, National Science Foundation Office of Polar Programs, and data collection protocols were approved by Point Blue and Oregon State University’s Institutional Animal Care and Use Committees. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the US Government.

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