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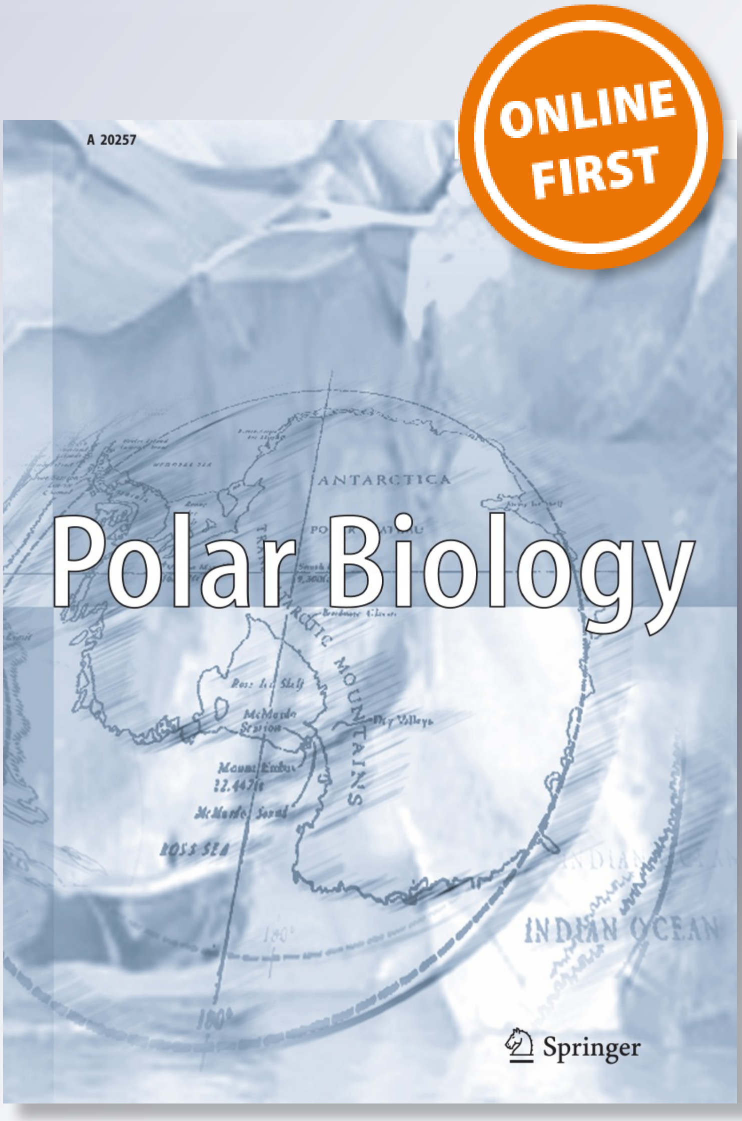

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ORIGINAL PAPER

Heat loss and site-dependent fecundity in chinstrap penguins (*Pygoscelis antarctica*)

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Abstract We studied the effects of heat loss and nest site quality on fecundity in a chinstrap penguin (*Pygoscelis antarctica*) colony on Deception Island, Antarctica. During the austral summers of 1990–1991, 1993–1994, and 1995–1996, 441 randomly selected nests were analyzed. Penguins breeding in the center of subcolonies hatched significantly earlier and had larger broods and than those nesting near or at the edge of the subcolonies. These differences, however, were significantly affected by interaction between year and nest location, being highly significant in colder years, when peripheral nests produce fewer young. Analysis of the rate of heat loss showed that penguins breeding at the edge of subcolonies lost heat twice as rapidly as those breeding in the interior of the subcolony. In a re-occupation experiment, evacuated center nests were re-occupied almost ten times as rapidly as edge nests. An analysis of mean fecundity in the period 1991–1996 and mean wind chill suggested that most of the variability in fecundity among years was related to differences in the rate of heat loss. Subcolonies tend to be as circular as possible, thereby decreasing the proportion of edge nests as the size of subcolony increases. Our results support the site-dependent fecundity hypothesis.

Keywords *Pygoscelis antarctica* · Site dependent fecundity · Wind-chill · Nest location · Nest selection

Introduction

Regulation of bird population size, especially through differences in fecundity, is well described (Ferrer and Donazar 1996; Rodenhouse et al. 1997; Newton 1998; Penteriani et al. 2003a; Kokko et al. 2004; Ferrer et al. 2006; 2008). Operating mechanisms underlying such regulation, however, often are unclear. Two major hypotheses have been proposed (Fretwell and Lucas 1970). Density-dependent patterns in mean fecundity could arise either by a higher proportion of individuals occupying poor quality habitats in a heterogeneous environment at high population densities (Andrewartha and Birch 1954; Pulliam and Danielson 1991; Dhondt et al. 1992; Ferrer and Donazar 1996; Krüger and Lindström 2001) or by individuals adjusting their behavior in response to changing densities within the same habitat (Lack 1954; Both 1998).

The first mechanism is the so-called site-dependence hypothesis (Dhondt et al. 1992; Ferrer and Donazar 1996; Rodenhouse et al. 1997). According to this hypothesis, individuals select optimal sites at low population densities. As density increases, an increasing proportion of individuals is relegated to lower-quality sites, and because of this, mean population fecundity declines (Andrewartha and Birch 1954; Brown 1969; Rodenhouse et al. 1997). The second mechanism is the so-called interference competition hypothesis. According to some authors

M. Ferrer (✉)
Estación Biológica de Doñana, CSIC, Avd. Americo Vespucio, 41092 Sevilla, Isla de la Cartuja, Spain
e-mail: mferrer@ebd.csic.es

J. Belliure
Departamento de Ecología, Universidad de Alcalá, Campus Universitario, 28871 Alcalá de Henares, Madrid, Spain

E. Minguez
Parque Natural Serra Gelada y Entorno Litoral, Paseo de la Carretera 34, 03501 Benidorm, Alicante, Spain

E. Casado
Fundación Migres, Inca Garcilaso, 1. Edificio REE, 41092 Sevilla, Isla de la Cartuja, Spain

K. Bildstein
Acopian Center for Conservation Learning, Hawk Mountain Sanctuary, 410 Summer Valley Road, Orwigsburg, PA 17961, USA

(Lack 1966; Fretwell and Lucas 1970 Dhondt and Shillemans 1983), density-dependent depression of fecundity can arise from an increased frequency of aggression, interference among territorial pairs, or both factors resulting in a hostile social environment that leads to a relatively uniform decrease in bird performance. According to the latter hypothesis, as densities increase, all individuals should show reduced fecundity.

If site dependence is occurring, we expect to find significant differences depending on site location in poor years, but less or no difference in good years (Ferrer and Donazar 1996; Ferrer et al. 2006, 2008). If interference is occurring, we expect to find no differences among site locations, regardless of annual variations in environmental conditions. Another possible alternative could be that both hypotheses may be operating at the same time (i.e., they are not mutually exclusive). That said, we could find data consistent with both sets of proposed predictions

Several examples of site-dependent fecundity have been documented for territorial species (Dhondt et al. 1992; Ferrer and Donazar 1996; Krüger and Lindström 2001), but few have been documented for colonial-nesting species (but see Kokko et al. 2004). That said, colonial-nesting species, particularly seabirds, offer an interesting opportunity to analyze site-dependent fecundity because their nests usually are very close to each other, and we can discard other possible confounding factors that might affect fecundity in more territorial species (i.e., habitat features not controlled for in the analyses).

The site-dependent hypothesis assumes that individuals are able to discriminate adequately the quality of the site. This basic assumption, however, is seldom tested (Kokko et al. 2004).

Here, we report on site-dependent fecundity of chinstrap penguins (*Pygoscelis antarctica*), a species that is long-lived, easily observed, and extremely site faithful. The "nest territory" consists of the nest site itself, with physical properties that do not vary much among years. Feeding opportunities do not depend on characteristics of nest site, and fecundity is easy to measure. Due to the harsh climate of Antarctica, heat loss and energy expenditure are relevant factors potentially affecting breeding output in a colony (Bevan et al. 2002; Green et al. 2002). Because of this, we examined differences in rates of heat loss among nests.

We tested the site-dependent hypothesis by examining the relationship between fecundity and nest-site characteristics, and variations in fecundity among years. We also evaluated whether penguins are able to discriminate the relative quality of different nest sites.

Materials and methods

Study colony, nest position, phenology, and fecundity

The study was conducted at the Vapour Col chinstrap penguin colony (approx. 20,000 breeding pairs) on Deception Island, South Shetlands, Antarctica (63°00′S, 60°40′W, Fig. 1). Most experiments were conducted in the 1995–1996 austral summer, but we also used fecundity data from the same rookery recorded during the austral summers of 1990–1991, 1993–1994, and 1995–1996 (hereafter 1991, 1994, and 1996, respectively). Chinstrap penguins breed on the ground in dense aggregations at the subcolonies, with inter-nest distances averaging about 1 m. Chinstrap penguins are a medium-sized penguin (around 4 kg) with a maximum clutch size of two eggs. The only obvious resource in the territory is the nest site itself.

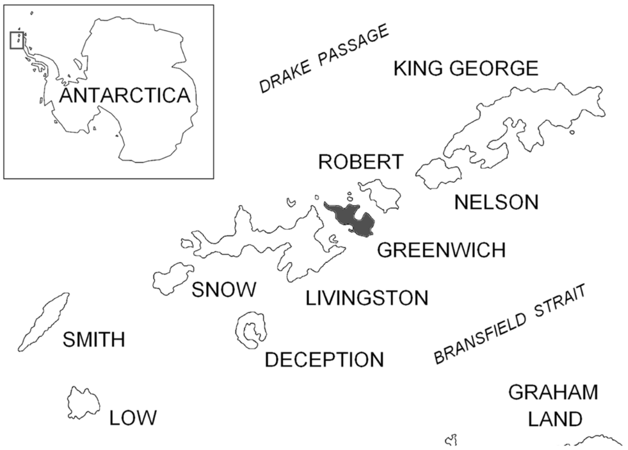

Fig. 1 Map of the study area. The colony was in Deception Island, close to Antarctic Peninsula

During the three breeding seasons, 441 nests (131 in 1991, 162 in 1994, and 148 in 1996) were selected and marked with numbered sticks at the end of the incubation period, and adults were tagged with metal flipper tags (standard 34 × 17 mm penguin bands, produced by Lambournes Ltd, Solihull, UK). Only occupied nests with at least one egg were considered in our sample. We sampled five subcolonies with more than 150 breeding pairs each. The nests we selected were in different areas in the subcolonies. Nests were selected haphazardly within each of the three following categories of "nest location": "edge," where nests occupied locations in the external ring of nests in the subcolony; "center," where nests were at least two nests away from the subcolony edge; and "sub-center," where nests were surrounded by nests, but at least one of those nests was an "edge" nest and at least one was a "center" nest. Distances between center and edge selected nests ranged between 8 and 21 m depending of the size of the subcolony.

We attempted to visit nests daily before hatching. As hatching is normally asynchronous in this species (modal asynchrony = 1 day, Moreno et al. 1994), we used the date of the first hatching as the brood-hatching date. During periodic visits after hatching (daily whenever possible), we recorded the survival of the chicks until 15 days of age, when they are first able to thermoregulate independently (Taylor 1985). Fecundity was defined as the number of 15-day-old nestlings per study nest.

Nest temperature, disturbance, and predation rates

In 1996, we also conducted several observations and experiments in order to ascertain the quality of nest sites (as related to fecundity and location) and individual's ability to detect it. Deception Island is part of a geologically dissected system, and the surface of the colony exhibited thermal anomalies of up to 11 °C. Using a digital thermometer model Fluke, K/j 52, and waiting 2 min until temperatures stabilized, we recorded the ground temperature in 147 nests inside the study subcolonies including the three types of nest-site locations. All measurements were taken before hatching in two-egg nests, at the same hours during days of similar conditions of wind and temperature trying to randomize the order of nest site visited (December 14–16, 1995).

We also measured the rate of heat loss in 132 randomly selected nests, using a thermometer inlayed in a 4 × 7 × 1 cm thick methacrylate. The thermometer was warmed to 35 °C, then left on the ground, 20 cm from the nest border, in the direction of the wind. We recorded the time in seconds it took the temperature to fall from 30 to 20 °C. All measurements were made across 2 days with similar conditions of wind and temperature (December 12–13, 1995, mean temperature = 3 °C; mean wind speed = 11 km/h). All selected nests were placed on flat areas without any protection from the wind. We took only one measurement in each nest. We also conducted observations ($n = 173$ nests) of the number of interactions between nest owners and other adults in transit during incubation. At each focal nest, we recorded how many adults passed at shorter distances than half the mean of inter-nest distance (0.5 m) and how many of them showed aggressive interactions with the owner, also recording the number of times the incubating penguin stood up, exposing its eggs to ambient temperatures. We use 15-min observation periods, totalling 44 h of observation (observations made December 14–19, 1995).

To determine whether penguins were able to assess the quality of nest sites, we selected 56 previously abandoned nests that had been re-occupied by non-breeding individuals (typically young males). We moved the individual defending the nest to a distance of 10 m, clearing the nest site of stones (most abandoned and re-occupied nests had no stones) to avoid any "stone effects" in the evaluation of quality by penguins (Moreno et al. 1995) and recorded the time in seconds until the nest was re-occupied by a different penguin. The penguins came from the pool of them that are usually moving by the edge of the subcolonies. We never recorded any penguin from surrounding nests trying to occupy the evacuated nests.

Additionally, we used meteorological data recorded on the island by the National Institute of Meteorology of Spain, including temperature (minimum and maximum), wind speed (mean and mean of maximum gusts), humidity, and precipitation. Using these data, we calculated wind chill using mean of maxima gusts and the following formula:

$$T_s = 13.12 + 0.6215 \times T - 11.37 \times V^{0.16} + 0.3965 \times T \times V^{0.16}$$

In this equation T_s is wind chill in °C, T is air temperature, and V is wind speed in Km/h (National Weather Service, USA: http://www.nws.noaa.gov/om/windchill/index.shtml). We used means of each month of meteorological parameters as well as published fecundity parameters of this rookery (number of chicks ≥15 day old; de León 2000) for the period 1991–1996, to correlate wind chill data with fecundity parameters. Meteorological data from December, January, and February of each austral summer were used in order to coincide with incubation and early chick rearing (before chicks are able to thermoregulate).

Finally, as differential predation risk has been associated with location of the nest in the subcolony (Davis et al. 1989; Forster and Phillips 2009), we performed specific observations of the behavior of great skuas (*Catharacta skua*). We conducted observations from vantage points near the colony over 26 h on five different days homogeneously distributed throughout the study period, continuously following each focal individual, and recording their feeding behavior (Penteriani et al. 2003b).

Subcolony shape

We analyzed the shape of subcolonies to test predictions about area/perimeter ratios. We recorded distribution of nests in the three categories of "nest location" in 13 subcolonies, ranging from 96 to 1607 nests. Using these subcolonies, we analyzed the relationship between subcolony size (total number of nests) and the rate of edge nests per total nests, in order to test whether subcolonies tend to fit a circular form. Additionally we calculated the expected relationship between edge nests versus total nests in theoretical perfect circle with increasing number of nests.

Statistical analyses

We used generalized linear models (GLMs) to perform most of the parametric analyses. Fecundity parameters (hatching date, number of chicks, number of chicks surviving to 15 days) were treated as dependent variables, with nest location, year, and the interaction between these terms were treated as factors. To analyze the relationship between brood-hatching date and nest location, we used a normal distribution and log link function in a GLM with brood-hatching date as the reply variable, and year, nest location, and the interaction of year and location as explanatory variables. GLM was also performed to analyze clutch size as a reply variable with the same explanatory variables in the model, but using a binomial distribution (1 or 2 as possible values) and logit link function. Brood sizes at day zero as well as day 15 after hatching also were analyzed with GLMs using multinomial distribution (0, 1, and 2 chicks as possible values) and logit link function.

To analyze the effect of nest location on disturbance measures (frequency of adults in transit, numbers of aggressive interactions, frequency of egg exposure), we used GLMs with Poisson distribution and log link function. Gamma distribution and log link function were used in GLM with the rate of heat loss as the reply variable and location as explanatory factor. To account for the possible effect on fecundity of differences in heat loss among locations, we conducted a GLM with a multinomial distribution and logit link function using number of 15-day-old chicks in the brood as the reply variable, and nest location and rate of heat loss as explanatory variables, using the 132 nests from the heat loss measurements in 1996. Again, GLM with gamma distribution and log link function was used to analyze the effect of nest location on re-occupation time after evacuation. All distributions of residual were tested for normality using Kolmogorov–Smirnov test or Shapiro–Wilk test as appropriate being all normally distributed.

A linear regression was performed to analyze the relationship between mean fecundity records and wind chill (mean values for the 3 months of each summer). Statistica 7.0 software statistical package was used to perform statistical procedures, and we used an alpha value of 0.05 to assess significance of results.

Ethical standards

Procedures used in this study comply with the current laws for working in Antarctica. Permission to work in the study area and for penguin handling was granted by the Spanish Polar Committee.

Results

Nest position, phenology, and fecundity

Table 1 Summary of fecundity parameters (number of eggs in the nest, 1-day-old chicks, 15-day-old chicks, and sample size) recorded in the chinstrap penguin colony by year and nest location inside the subcolony

Year	Location	N. Eggs (SD)	1-day chicks (SD)	15-day chicks (SD)	*N*
1991	Center	1.958 (0.8)	1.724 (0.5)	1.437 (0.6)	48
	Subcenter	1.847 (1.1)	1.282 (0.5)	1.173 (0.7)	46
	Edge	1.729 (0.4)	1.054 (0.6)	0.945 (0.6)	37
1994	Center	1.966 (0.8)	1.766 (0.5)	1.466 (0.6)	60
	Subcenter	1.901 (0.8)	1.764 (0.5)	1.294 (0.6)	51
	Edge	1.882 (1.1)	1.725 (0.3)	1.274 (0.7)	51
1996	Center	1.981 (0.9)	1.833 (0.5)	1.388 (0.7)	54
	Subcenter	1.872 (1.1)	1.744 (0.5)	1.276 (0.6)	47
	Edge	1.808 (0.2)	1.638 (0.4)	1.234 (0.7)	47

We found a significant relationship between nest location and hatching date, with central nests hatching earlier than subcenter and edge nests [GLM; center = 3.11 (SE = 0.19); subcenter = 3.73 (SE 0.21); edge = 5.07 (SE 0.27); Wald statistic = 44.04, $P < 0.001$)]. No significant effect of the year was found [GLM; 1991 = 3.86 (SE 0.25); 1994 = 3.99 (SE 0.22); 1996 = 3.90 (SE 0.23); Wald statistic = 0.51, $P = 0.775$]. Interaction between year and location showed a significant effect in hatching dates, with the edge nests hatching later in 1991, the coldest year (GLM; year × nest location; Wald statistic = 23.23, $P < 0.001$) Clutch size was not significantly affected by nest location (GLM; Wald statistic = 3.25, $P = 0.196$). Neither year (GLM; Wald statistic = 1.57, $P = 0.454$) nor interaction between year and location (GLM; Wald statistic = 2.88, $P = 577$) showed significant effects.

A significant relationship between number of chicks per nest and nest location was found, with center nests having larger broods (GLM; center = 1.79; subcenter = 1.61; edge = 1.51; Wald statistic = 21.41, $P < 0.001$, Table 1). Year also showed a significant effect on brood size (1991 = 1.34; 1994 = 1.75; 1996 = 1.74; Wald statistic = 10.99, $P = 0.026$), as well as year and location interaction (Wald statistic = 17.28, $P = 0.027$). Mean number of 15-day-old chicks per nest was significantly affected by nest location, with the highest values were found in center nests (GLM; center = 1.43; subcenter = 1.25; edge = 1.17; Wald statistic = 11.39, $P = 0.024$). Year showed significant effect on brood size (GLM; 1991 = 1.20; 1994 = 1.35; 1996 = 1.30; Wald statistic = 15.57, $P = 0.003$) as well as year and location interaction (Wald statistic = 17.61, $P = 0.022$). When we included only the center nests in the analyses, no difference in brood size among years was detected (GLM; Wald statistic = 1.34, $P = 0.853$). On the other hand, highly significant differences arose when only edge nests were included in the analysis (GLM; Wald statistic = 26.02, $P < 0.001$).

Nest temperature, disturbance, and predation rates

Ground temperature at active nests oscillated between 0 and +11 °C, with a mean value of +6.02 °C. No relationship was found between ground temperature at the nest and the number of 15-day-old chicks at the nest (GLM; Wald statistic = 1.87, $P = 0.392$). In addition, no significant difference in ground temperature according nest locations was found (GLM; center = 5.33 (SE 0.53); subcenter = 5.96 (SE 0.51); edge = 5.11 (SE 0.53); Wald statistic = 0.252, $P = 0.881$).

We found highly significant differences in frequency of adults in transit among nest locations (GLM; Wald statistic = 167.63, $n = 176$, $P < 0.001$), with many more adults passing near edge nests than center nests (adult in transit/15 min; center = 0.46, subcenter = 1.25, edge = 3.98). Numbers of aggressive interactions also differed significantly among the three types of nests (GLM; Wald statistic = 28.89, $n = 176$, $P < 0.001$), being more frequent in edge nests than in subcentral and center nests (aggressive interactions/15 min; center = 0.42, subcenter = 1.05, edge = 1.38). Frequency of eggs exposure to the air temperature varied by nest location (GLM; Wald statistic = 25.70, $n = 176$, $P < 0.001$), with edge nests exhibiting a higher frequency of exposure than center nests (Fig. 2a).

Rate of heat loss in the 132 analyzed nests varied significantly with location (GLM; Wald statistic = 68.70, $n = 132$, $P < 0.001$), with edge nests showing higher rates of heat loss than subcenter and center nests (Fig. 2b).

Re-occupation time after evacuation of non-reproductive penguins differed significantly among nest types (GLM; Wald statistic = 74.71, $n = 56$, $P < 0.001$). Time to re-occupation by a different penguin was shorter in center nests than in subcenter or edge nests (Fig. 2c).

During the 26 h of observation of skuas, we observed three predation attempts on eggs (one of which was successful). We never observed any attempt by skuas on a chick, regardless of the latter's body size. During the observations made on individual skuas, we observed this species feeding on carcasses of already-dead chicks or adults only.

Fecundity and weather

A significant relationship between fecundity and mean temperature was found, with higher fecundity records as temperature increased ($r = 0.853$; $P = 0.030$). Similar results were obtained using mean of minimum temperatures ($r = 0.842$; $P = 0.035$). Nonsignificant relationships were found between fecundity and wind speed ($r = 0.131$; $P = 0.803$) or mean of maximum gusts ($r = -0.424$; $P = 0.402$).

For the period 1991–1996, a highly significant relationship between mean wind chill and mean fecundity of the colony was found ($r = 0.991$, $P < 0.001$; Fig. 2), with fecundity increasing with increasing wind chill, i.e., when effective temperature was higher. This result supports the idea of wind chill driving overall (colony-wide) fecundity, not only differences according nest location inside the same subcolony (Fig. 3).

An subcolonies shape

We counted 6,326 occupied nests in the 13 sampled subcolonies with 1,347 being edge nests (21.29 %). The smallest subcolony was composed of 96 nests with 46 of them being edge nests (48 %), 30 subcenter, and 20 center nests. In the largest subcolony that we counted, there were 1,607 nests with 268 (16.7 %) of them edge nests, 205

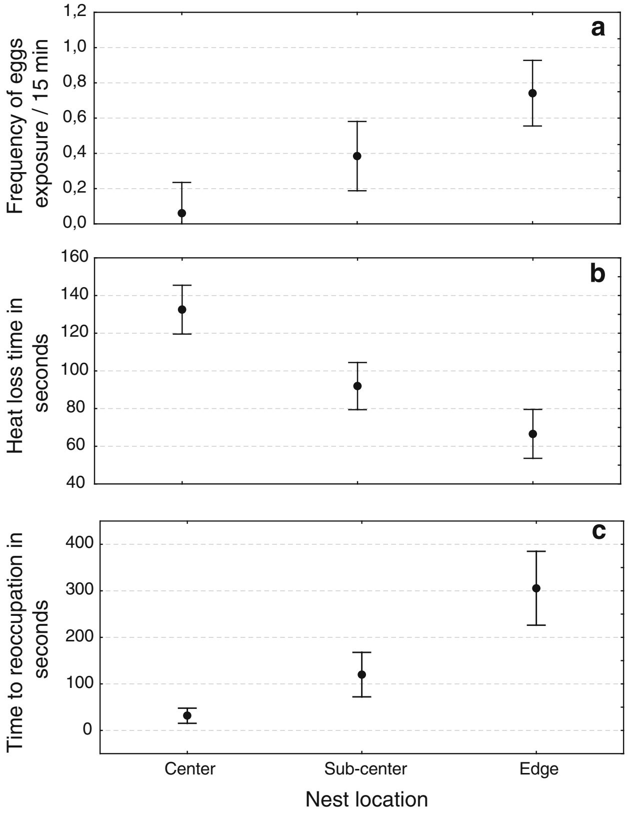

Fig. 2 Differences among nest locations in the frequency of eggs exposure to ambient temperatures due to interferences in 15-min interval (**a**), rate of heat loss measured as time in seconds to fall from 30 to 20 °C (**b**), and re-occupation time (in seconds) after a non-breeding penguin occupying a nest was evacuated (**c**). Significant differences among nest position in the subcolony were detected in the three variables. *Vertical bars* denote 0.95 CIs

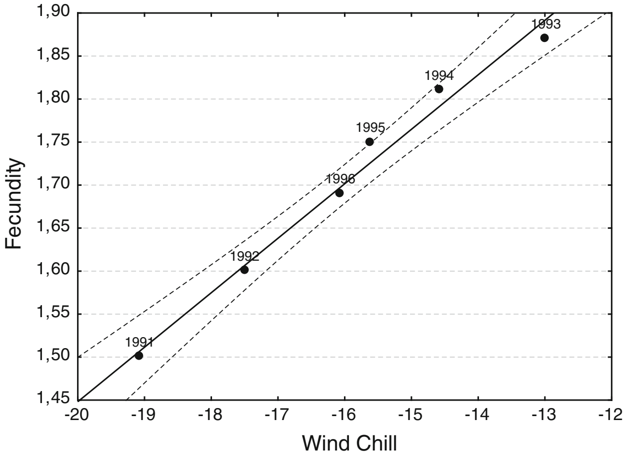

Fig. 3 Relationship between mean fecundity (number of chicks older than 15 days per breeding pair in the colony) and mean December–February wind chill. A significant positive linear relation was found ($r = 0.991$, $P < 0.001$), with high fecundity in years with less severe wind chill (*dotted line* 95 % CI)

subcenter, and 1,134 center nests. A significant relationship between subcolony size and proportion of edge nests was found, with peripheral nests representing a lower proportion of the subcolony as subcolony size increased ($r = -0.693$; $P = 0.008$, Fig. 4). The expected relationship between subcolony size and proportion of peripheral nests in perfectly circular subcolonies is shown in Fig. 4. The trend in the real subcolonies was similar to that of ideal circle, supporting the idea of subcolonies being as close to circular as possible.

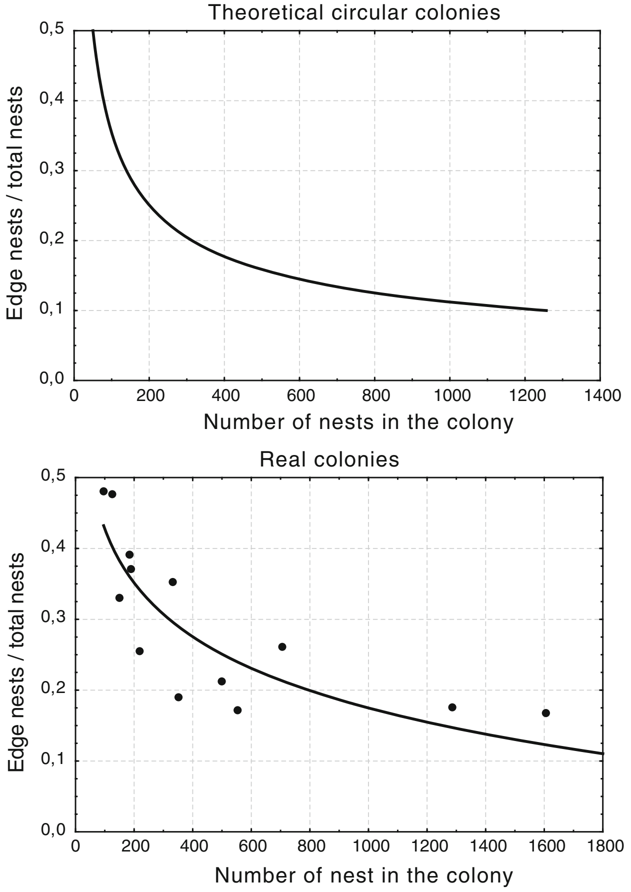

Fig. 4 Relationship between subcolony size (total number of nests) and the proportion of edge nests per total nests. *Upper graph* shows theoretical perfect circular subcolonies and *lower* one the 13 real subcolonies of the present study ($r = -0.693$; $P = 0.008$)

Discussion

We found highly significant differences in breeding performances among the three nest locations (i.e., center, subcenter, and edge nests). Penguins breeding in the center of the subcolony hatched earlier than did those nesting at or near the edge of the subcolony. Differences in hatching dates were greater in 1991 between center and edge nests than in the other 2 years. Center nesters also had larger broods when the chicks were 0 day old and 15 days old. These differences, however, were significantly affected by an interaction between year and location. In 1991, the colder year of the study, differences between center and edge nests were greater than in the other 2 years. Importantly, when only center nests are considered in the analyses, the year effect disappears. On the other hand, the year effect is highly significant for edge nests. During low-fecundity years, penguins breeding at the edge of colonies have lower production, whereas those breeding at the center of the subcolony produce more or less the same numbers of chicks in both "low" and "high" fecundity years.

Perhaps due to this episodic year effect, other researchers have been unable to find differences in fecundity among nest locations based on a single year study (Barbosa et al. 1997) or only find differences in certain years (Descamps et al. 2009). As predicted by the site-dependent hypothesis, we found a highly significant effect of the interaction between year and nest location. As the site-dependent fecundity hypothesis predicted, differences according to site quality must be large in poor years but small or no different in good years (Ferrer and Donazar 1996; Ferrer et al. 2006, 2008). As no significant differences among sites according the quality of the year are expected under interference hypothesis, our results support the site-dependent fecundity hypothesis as the principal mechanism acting on fecundity differences in this population.

Alternatively, it can be argued that in poor years, interference may have strong effects due to the general increases in competition for a limited set of resources. That said, this does not predict that the effect would be greater in certain sites than in others. For us, the most reasonable explanation for our results includes preexisting differences in site quality that determines any possible spatial structure in individual quality occupying them. The fact that penguins select center nests more than the other two categories in the re-occupation experiment strongly support site quality as the main driver of fecundity in our colony.

Age composition of birds often affects breeding performance (Tenaza 1971; Ainley et al. 1983; Ens et al. 1995 but see Ferrer and Bisson 2003). Some studies point to younger and more inexperienced breeders occupying the peripheral positions (Spurr 1973; Ainley et al. 1983; Robertson 1986). We had no information about age and experience of individuals in our colony. Although we cannot discard an inherent age effect associated with nest location, our results show that central nests are more rapidly reoccupied than the other two categories. Edge nests are more disturbed than center and subcenter nests, and edge nests experienced higher rate of heat loss than subcenter and center nests, and lower breeding success in cold years, all of which supports the notion that location is an important factor driving fecundity in this colony.

Whereas adults have longer and deeper bills than yearlings (Minguez et al. 1998), birds in central nests did not show longer bills but only deeper bills, that is, stronger bills than peripheral breeders (Minguez et al. 2001). This suggests that they may have achieved their central positions competitively regardless of age, as chinstrap penguins fight with other conspecifics using the bill as a weapon. Even so, a possible effect of differences in individual quality or age, occupying different locations should not be discarded (Wilson and Nussey 2009; Descamps et al. 2009). Nevertheless, it is necessary to assume a preexisting difference in quality among nest locations to generate a difference in the quality of individuals occupying them.

An additional mechanism generating differences in fecundity between center, subcenter, and edge nests could be differential predation pressure among nest locations (see Jackson et al. 2005). Predation by skuas has been proposed as one of the main proximate causes of differences in fecundity among sites in sea bird colonies (Davis et al. 1989; Emslie et al. 1995; Forster and Phillips 2009). Our results, however, show that predation by skuas had no influence on the differences we observed. In fact, the carcasses of chick and adult chinstraps, as well as abandoned eggs, were the main food of the skuas living close to the colony, due to their high frequency and the low deterioration rates (M. Ferrer, unpublished data). This kind of feeding behavior, justified by the lower energy expenditure and ease of gathering of carcasses, compared with more difficult, risky, and energy-demanding active predation seems to be relatively common in skuas.

Finally, it remains possible that Vapour Col rookery represents an unusual situation in Antarctica, because a relatively low number of skuas (estimated number of 6–7 pairs near the rookery, plus an unknown number of longer-distance breeding pairs visiting the rookery) inhabits a huge concentration of penguin pairs (ca. 20,000). Thus, easy food in the form of carrion may be plentiful, and this could explain the absence of predation attempts on eggs and chicks.

A critical assumption of the site-dependent hypothesis is that individuals are able to assess correctly the quality of the site; otherwise, the occupations would be at random even if a difference in quality among sites exits. Our re-occupation experiment provides evidence that they do. Evacuated center nests were re-occupied almost ten times more rapidly than edge nests suggesting that penguins prefer to occupy the nest in sites with better characteristics and they know where they are.

Our results raise the question of why birds in the edges of the colony are less productive in poor years. The observations and experiments conducted at the colony provide an explanation. Temperature of the ground seems not to play an important role. The distribution of thermal anomalies is at a different scale than center and edge zones of the subcolonies. In contrast, the extent of interactions among penguins shifts from the center to the edge of the subcolony, with edge nesters more likely to be disturbed (up to eight times more) than center nesters. These disturbances would be especially dangerous when eggs are exposed to ambient temperatures, a circumstance that occurred more than 12 times more frequently at the at edge nests than at center nests. Assuming that lower air temperatures and higher wind speeds affect penguins negatively, fecundity effects can be expected. As a subcolony increases in size, disproportionately more penguins pass through edge nests, increasing the unfavorable effects of these interactions. This, in turn, may be an important limiting factor constraining subcolony size. Finally, we note that the effects of wind chill on fecundity output have been reported in other bird species (Reid et al. 2002; D'Alba et al. 2009).

Our rate of heat loss data clearly demonstrates that penguins breeding at the edge lost heat twice as rapidly those breeding in the interior of the subcolony. These differences would be because center nests are more protected from the wind by their neighboring penguins. This suggests that birds on the edge nests experienced higher risk of get their eggs or chick chilled and greater energy expenditure in self-maintenance or both. The magnitude of differences among sites depends upon wind chill and is expected to be greater in cold years (1991 in our case). In fact, a large quantity of un-hatched eggs was observed surrounding the colony especially in 1991. As the size of the subcolony increases, disproportionately fewer nests are at the edge, so a high proportion of breeders is protected against wind chill. This phenomenon could act to increase the size of individual subcolonies. For this reason, among others, subcolonies tend to be as circular as possible; decreasing the proportion of exposes edge nests.

The analysis of mean fecundity in the period 1991–1996 and the mean wind chill suggests that part of the variability in overall fecundity among our years of study was related to increases in the rate of heat loss for edge-nesting individuals. We cannot rule out other potential explanations correlated with temperature and wind chill, like sea ice extent, changes in availability of krill, etc. It is possible that younger or lower-quality individuals occupy edge nests and were negatively impacted by several factors coincident with colder temperatures, but our results support the conclusion that site quality (linked to location) plays an important role driving fecundity for this chinstrap penguin colony.

Finally, our findings have implications in the context of global climate change (Ainley 2002). If temperatures warm in the region, the effect we described is likely to diminish. One way of testing this would be to look at the degree of circularity in subcolonies of chinstrap and other species of penguins in areas of severe and less severe weather. Some predictions would be that circularity diminishes, subcolony sizes tend to shrink, and the number of subcolonies to increase as wind chill becomes less severe.

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