

SUBCOLONY CHARACTERISTICS AND BREEDING PERFORMANCE IN THE CHINSTRAP PENGUIN *PYGOSCELIS ANTARCTICA*

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SUMMARY.—*Subcolony characteristics and breeding performance in the chinstrap penguin Pygoscelis antarctica.*

Aims: Subcolonies of penguins differ markedly in physical characteristics and in breeding success. Subcolony size is the best studied subcolony characteristic and has been suggested to be an important factor explaining the variation in reproductive success. Small subcolonies generally have lower breeding success, probably because they suffer from worse environmental conditions. It is likely that lower quality individuals also occupy smaller subcolonies, which in turn affects breeding success. However, results are not always consistent, and other subcolony characteristics may mediate breeding success. In the present study, the relationship is investigated between physical subcolony characteristics (slope, isolation and size) and several variables indicative of individual quality and breeding success in the chinstrap penguin *Pygoscelis antarctica*.

Location: The study was performed in the Vapour Col chinstrap penguin colony on Deception Island (South Shetlands Archipelago, 63° 00' S, 60° 40' W) during the austral 2002-03 breeding season.

Methods: The slope, the degree of isolation and the size (number of nests) of 22 randomly selected subcolonies were measured. Variables indicating individual quality were considered in 10 nests of each subcolony: parental body size (bill length, bill depth, flipper length), nest size and egg size, and variables indicating breeding success: hatching date and hatching success.

Results: Both isolated and sloped subcolonies were smaller in size, and were occupied by male parents with shorter bills and less bill depth respectively. Isolated subcolonies also showed a delayed hatching date and lower hatching success and females of more sloped subcolonies laid smaller eggs. Nest size was larger in isolated subcolonies and smaller in sloped subcolonies.

Conclusions: This study indicates that physical characteristics of subcolonies, such as the degree of isolation and slope, rather than just size, affect breeding success of chinstrap penguins. It is also suggested that nest size could be an indicator of individual quality only if it is compared within the same subcolony or if the effect of subcolony is taking into account.

Key words: colonial breeding, nest placement, penguins, egg size, bill size, flipper length, hatching date, hatching success, nest size.

RESUMEN.—*Características de las subcolonias y reproducción en el pingüino barbijo Pygoscelis antarctica.*

Objetivos: Los núcleos reproductores o subcolonias de pingüinos difieren llamativamente en las características físicas que las conforman y en el éxito reproductor de los individuos que las ocupan. El tamaño de la subcolonia es una de las características más estudiadas y que supuestamente más influye en la va-

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riación del éxito reproductor entre subcolonias. Las subcolonias más pequeñas suelen presentar un menor éxito reproductor, probablemente porque las condiciones ambientales, como el riesgo de depredación, juegan en su contra. Es por lo tanto previsible que subcolonias más pequeñas estén ocupadas por individuos de peor calidad lo que afecta a su vez el éxito reproductor. Sin embargo no siempre los resultados de los estudios son consistentes. Otras características físicas podrían mediar en la calidad parental y el éxito reproductor. En este estudio se investiga la relación entre características de las subcolonias (pendiente, aislamiento y tamaño) y variables indicativas de la calidad individual y éxito reproductor en el pingüino barbijo *Pygoscelis antarctica*.

Localidad: Este estudio se llevó a cabo en la colonia de pingüinos barbijos de Vapour Col en la isla Decepción (archipiélago Shetlands del Sur, 63° 00' S, 60° 40' W) durante el verano austral de 2002-03.

Métodos: Se midió la pendiente, grado de aislamiento y tamaño (número de nidos) en 22 subcolonias elegidas al azar. En 10 nidos de cada subcolonia se midieron indicadores de calidad individual de sus ocupantes (longitud de la aleta y pico, alto de pico, tamaño del nido y del huevo) e indicadores de éxito reproductor (fecha de eclosión, éxito de eclosión).

Resultados: Las subcolonias más aisladas e inclinadas también fueron más pequeñas y estuvieron ocupadas por machos con picos más cortos y menos altos respectivamente. Las subcolonias más aisladas también mostraron una fecha de eclosión más tardía y un éxito de eclosión menor. Las subcolonias más inclinadas estuvieron ocupadas por hembras que pusieron huevos más pequeños. El tamaño del nido estuvo correlacionado positivamente con el grado de aislamiento de la subcolonia y negativamente con la pendiente.

Conclusiones: Nuestro estudio evidencia que otras características físicas de las subcolonias, como la pendiente y grado de aislamiento, además del tamaño, parecen jugar un importante papel en la reproducción del pingüino barbijo. También se sugiere que el tamaño de nido podría reflejar calidad individual si su variación se mide dentro de una única subcolonia o si se corrige por el efecto de la subcolonia.

Palabras clave: reproducción en colonias, posición de nido, pingüinos, tamaño de huevo, tamaño de pico, longitud de la aleta, fecha de eclosión, éxito de eclosión, tamaño de nido.

INTRODUCTION

In colonial birds, like penguins, nest placement is important determining breeding success. This is because nest positions within the colony vary in environmental conditions, for example predation pressure or inclement weather (Tenaza, 1971; Gaston *et al.*, 1996; Barbosa *et al.*, 1997; Brunton, 1997; Stokes *et al.*, 1998; Massaro *et al.*, 2001; Velando *et al.*, 2002; Olmos, 2003). Penguins form dense nest aggregations, called subcolonies, separated from each other by ground not used for nesting (Williams, 1995). Reproductive success varies greatly among subcolonies, but the proximate and ultimate causes for this variation are unclear. Environmental conditions related to a noticeable variation in subcolony size have been put forward as the most important expla-

nation for variation in breeding success among subcolonies. Most studies found that penguins breeding in large subcolonies were more successful than those breeding in small subcolonies (Tenaza, 1971; Davis, 1982; Robertson, 1986; Young, 1994). However, this relationship was not clear in other studies (Hunter, 1991; Emslie *et al.*, 1995). Given these rather ambiguous findings, other physical characteristics of subcolonies, such as isolation and slope, may influence reproductive success.

Further, the relationship between environmental conditions of subcolonies and breeding success is most likely mediated by individual quality. Subcolonies offering better environmental conditions may be occupied by better parents, because these birds arrive first to the rookery (age-related effect: Ainley, 1983; Robertson, 1986), or occupy better nest sites

(Mínguez *et al.*, 2001). However, the relationship between subcolony characteristics and individual quality has not been studied yet.

In the present study, using information of active nests in 22 subcolonies of the Chinstrap Penguin *Pygoscelis antarctica*, the relationship is examined between physical subcolony characteristics (size, slope and isolation) and several variables known to be indicative of parental quality in chinstrap penguins: body size (De León *et al.*, 1998; Mínguez *et al.*, 2001), nest size (Fargallo *et al.*, 2001; Fargallo *et al.*, 2004), hatching date and hatching success (Viñuela *et al.*, 1996; Moreno *et al.*, 1997), and egg size (Belliure *et al.*, 1999). Previous studies in the chinstrap penguins investigated the effect of subcolony size on breeding success and nest size. Barbosa *et al.* (1997) found that large subcolonies showed better breeding success than small subcolonies. However, subcolony size had negative effects on nest size (Carrascal *et al.*, 1995; Barbosa *et al.*, 1997). Since the protection of eggs and small chicks against nest flooding is better in large than in small nests, nest size affects breeding success in chinstrap penguins (Moreno *et al.*, 1995; Fargallo *et al.*, 2001). This result of better breeding success, but smaller nests in large subcolonies raises further the question if other subcolony characteristics may additionally explain breeding performance in the chinstrap penguin.

MATERIAL AND METHODS

Study area and penguin sampling

The study was performed in the Vapour Col chinstrap penguin colony on Deception Island (South Shetlands Archipelago, 63° 00' S, 60° 40' W) during the austral 2002-03 breeding season. Chinstrap penguins breed in dense aggregations (subcolonies) separated from each other by ground not used for nesting. The Vapour Col colony is formed by approximate-

ly 22.500 breeding pairs nesting in 66 subcolonies with a mean size of 314 ± 47 nests (range: 5 to 1800 nests). Random selection was made of 22 subcolonies in the rookery, and the following physical characteristics of each subcolony recorded: (1) **subcolony size**: the number of breeding pairs (range: 24 - 1250 breeding pairs); (2) **subcolony slope**: the predominant (> 60 % of the nests) slope of the subcolony, using a 1 - 5 ranking, always estimated by the same researcher (1 = no inclination; 5 = maximum inclination, about 30°); (3) **subcolony isolation**: by means of photographs of the whole rookery the minimum distance between the outer border of the subcolony to the outer border of the 3 closest neighbouring subcolonies (range: 5 - 140m) was measured. The mean of these 3 measurements was used as an indicator of the isolation degree of the subcolony; (4) **neighbour subcolony size**: the mean number of breeding pairs in the nearest 3 subcolonies (range: 25 - 717 breeding pairs); (5) **distance to large subcolony**: the distance to the closest large (> 500 breeding pairs) subcolony (range: 5 - 550m).

Like in other penguin species (Tenaza, 1971; Young, 1994; Emslie *et al.*, 1995), chinstrap penguins breeding in peripheral nests hatched later than central breeders (Barbosa *et al.*, 1997). Even so, peripheral breeders of large subcolonies reached higher reproductive success compared to central breeders of small subcolonies (Barbosa *et al.*, 1997), thereby suggesting a linkage between subcolony size per se (physical characteristic) and breeding performance in this species. At the beginning of December (the middle of incubation), within each of the 22 subcolonies, 10 sample nests with the modal clutch size of 2 eggs (Viñuela *et al.*, 1996) were randomly selected along one axis extending from one border to the opposite border of the subcolony. In this way, peripheral and central nests were included in each sub sample of 10 nests, taking into account possible effects of nest placement within the sub-

colony on breeding success. Sample nests were marked with numbered stakes. Both parents were measured (bill depth, bill length and flipper length), egg size and nest size. Egg and bill measurements were taken with a sliding caliper to the nearest 0.01 cm, and flipper length with a metal rule to the nearest 1 mm. Egg size was calculated as the volume of an ellipsoid: $\frac{4}{3} \pi a b^2$ (cm³), where a is the largest radius and b the shortest. We used mean egg size of each nest in the analyses. Nest volume was calculated as the volume of a truncated cone (the pile of stones on the ground) minus the volume of a spherical segment (the cup): $\frac{1}{3} \pi H^2 (R^2 + rR + r^2) - \frac{1}{3} \pi h^2 (3r - h)$, where H is the height of the truncated cone, R is the outer radius, r is the inner radius and h is nest cup depth (Fig. 1). As real nests are irregular, H was estimated as the mean value of height measured in two opposite points (H₁ and H₂), R and r were estimated as the mean values of the radius positioned on two perpendicular axes (R₁ and R₂, r₁ and r₂). In previous studies, nest volume was estimated as nest weight (Moreno *et al.*, 1995; Fargallo *et al.*, 2001). This new procedure was faster and less stressing for penguins. The new method was validated by weighting 30 nests. Both estimations

were closely correlated ($r = 0.66$, $F_{1,29} = 22.87$, $P < 0.001$).

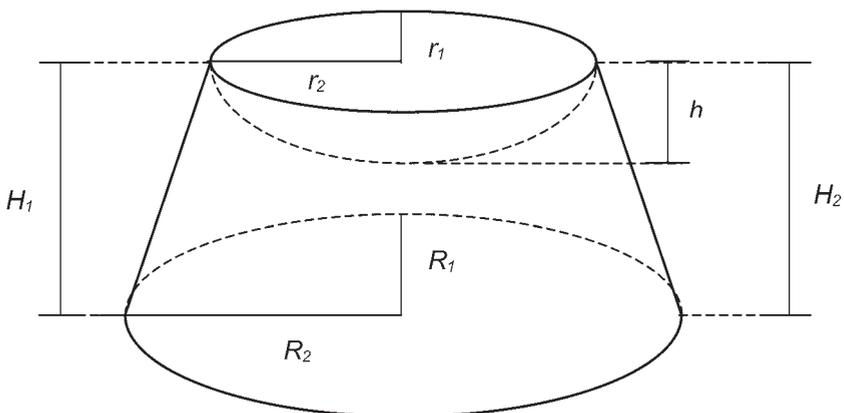
Chinstrap penguins are a sexually size dimorphic species in which males are larger than females (Amat *et al.*, 1993). Breeding individuals were sexed using the intra-pair difference in size, which was determined using the scores extracted from a discriminate function including bill depth, bill length and flipper length (Amat *et al.*, 1993). This method has been proved to be appropriate since Fargallo *et al.* (2004) sexed 96 % of breeding individuals correctly using this discriminate function.

Breeding phenology was estimated using hatching dates, defined as the first date in which any of the chicks was observed fully or partially out of the egg.

Statistical analyses

General Linear Mixed Models (GLMM, SAS 1989-96 Institute Inc., Cary, NC, USA) were used to explore if physical subcolony characteristics (explanatory variables) explained variation in nest size, egg size and hatching date (response variables), introducing the sub-

FIG. 1.—Schematic illustration of a hypothetical penguin nest, used to estimate nest volume in the field. [Esquema de un nido hipotético de pingüino y las distintas variables utilizadas para calcular su volumen en el campo.]



colony as a random factor. To explore the effect of explanatory variables on hatching success, we used a Generalized Linear Mixed Model (GLIMMIX), with each egg as unit (binary error: hatched versus not hatched, logarithmic link function). Subcolony and nest were random factors. Because parental size may also affect the response variables, all body size measurements were included of male as well as female parents as explanatory covariates into the model. In this way, the effects of subcolony characteristics were tested at the subcolony level, and the effects of parental body size measurements were tested at the nest level. Only if the subcolony did not account for any variation in the response variable (Restricted Maximum Likelihood method), subcolony characteristics were tested at the nest level (see degrees of freedom of egg size in Table 2), producing the same results as a General Linear Model (GLM). Type III tests calculated the significance of fixed effects. A forward stepwise procedure was used and tested the significance of each variable one by one, adding only the variable that resulted in the largest increase in model fit. The result is the most adequate model for explaining the variance in the response variable, where only significant explanatory variables are retained.

Furthermore, examination was carried out to see if physical subcolony characteristics (explanatory variables) predicted parental size measurements (bill length, bill depth and flipper length: response variables) using the same GLMM procedure as described above. Subcolony was again included in the model as a random factor to avoid pseudoreplication. Note that if the subcolony explained no variation in the response variable, the analyses were performed using the nest as unit, instead of the subcolony.

Nest size was log-transformed to meet a normal distribution; all other variables did not significantly differ from a normal distribution.

Degrees of freedom were calculated following the Satterthwaite method.

RESULTS

Subcolony characteristics

All the recorded physical characteristics of subcolonies were included in a Principal Components Factor Analysis (Table 1). The analysis produced two orthogonal factors. Factor 1 accounted for 43.8 % of variation among subcolonies, and was determined positively by the subcolony isolation and the distance to a large subcolony, and negatively by the neighbour subcolony size. High values of Factor 1 then indicate isolated subcolonies with very few breeding pairs in the closest neighbouring subcolonies. Factor 2 accounted for 28.6 % of variation and was positively determined by subcolony slope and negatively by subcolony size. Hence, high values of Factor 2 indicate small and highly sloped subcolonies. Note that subcolony size also tended to explain variation in Factor 1 (Table 1). In fact, a multiple regression showed that both factors were significantly negatively related to subcolony size ($R^2 = 0.54$, $F_{2,19} = 11.09$, $P < 0.001$; regression coefficient Factor 1: -0.49 , $P = 0.005$; regression coefficient Factor 2: -0.62 , $P < 0.001$). Thus, isolated and sloped subcolonies were also of smaller size.

Factor 1 was log-transformed to meet a normal distribution. We used these 2 factors as explanatory variables (representing the physical characteristics of subcolonies) in the GLMM models described in Material and Methods.

Nest size

Nest size was the only tested response variable which was significantly explained by both factors. More sloped subcolonies (*i.e.* subcolonies with higher Factor 2 values) contained significantly smaller nests than large and flat subcolonies (Table 2, Fig. 2A). Contrary, breeding pairs of isolated subcolonies (*i.e.* sub-

TABLE 1

Results of a Principal Components Factor Analysis explaining physical environmental variation among subcolonies. Factor loadings (Varimax raw) > 0.60 are marked (*).

[Resultados del Análisis de Componentes Principales que explica la variación física ambiental entre las subcolonias. Se marcan con un asterisco la saturación factorial (Varimax raw) mayores que 0,60.]

	Factor 1	Factor 2
Subcolony isolation [Aislamiento de la subcolonia]	0.78*	0.31
Neighbour subcolony size [Tamaño de la subcolonia más cercana]	-0.72*	0.34
Distance to large subcolony [Distancia a la mayor subcolonia]	0.92*	0.04
Subcolony slope [Pendiente de la subcolonia]	-0.05	0.91*
Subcolony size [Tamaño de la subcolonia]	-0.46	-0.62*
Eigenvalue [Eigenvalue]	2.19	1.43
% Total variance [Varianza total (%)]	43.8	28.6

colonies with higher Factor 1 values) built larger nests (Table 2, Fig. 2B). No parental size measurements were retained in the model and subcolony size was not related to nest size (GLMM: $F_{1,19,9} = 0.57$, $P = 0.46$).

Hatching date, hatching success and egg size

The degree of isolation, distance to a large subcolony and neighbour subcolony size (Factor 1) explained variation in hatching date and hatching success (Table 2). Subcolonies that experienced a higher degree of isolation and a low number of breeding neighbours hatched later and showed lower hatching success. No parental size measurements were retained in the models.

Subcolony slope and size (Factor 2) explained significant variation in egg size. Small subcolonies with a large slope contained, besides smaller nests, also smaller eggs (Table

2). In addition, female flipper length was also retained in the model to explain variation in egg size.

Parental size

Factor 1 was negatively related to male bill length (GLMM: estimate = -0.41, $F_{1,19,3} = 5.74$, $P = 0.027$). This means that males with shorter bills occupied more isolated subcolonies. Factor 1 did not explain significant variation in any other parental size measurement (all $P > 0.21$).

Factor 2 explained significant variation in male bill depth (GLMM: estimate = -1.14, $F_{1,210} = 4.30$, $P = 0.039$), but not in any other parental size measurement (all $P > 0.24$). This means that more sloped subcolonies were occupied by males with a smaller bill depth.

Bill depth between female and male of the same pair (controlling for subcolony) was positively correlated (GLMM: estimate = 0.19,

FIG. 2.—Relationship between mean subcolony nest size (cm^3 , log transformed) and A) the subcolony slope level (Factor 2), and B) the degree of subcolony isolation (Factor 1, log transformed).

[Relación entre el tamaño promedio de nido en las subcolonias (cm^3 , transformación logarítmica) y A) el nivel de pendiente de la subcolonia (Factor 2), y B) el grado de aislamiento de la subcolonia (Factor 1, transformación logarítmica).]

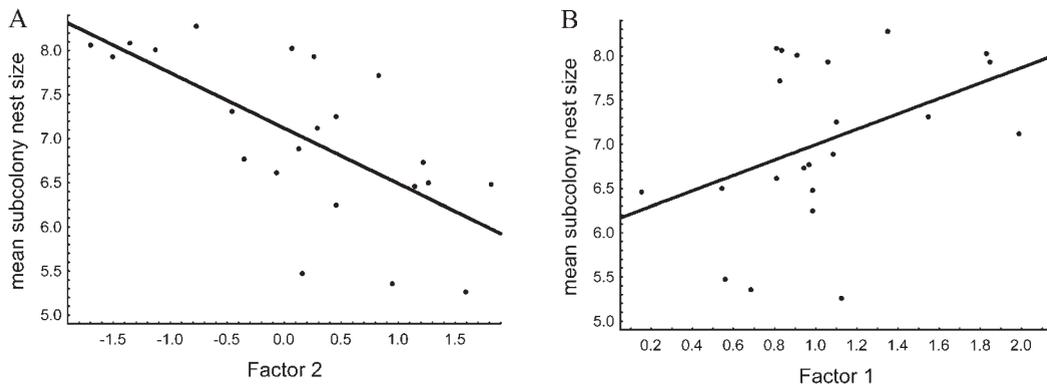


TABLE 2

Results of GLMM and GLIMMIX testing which subcolony characteristics (Factor 1: degree of isolation; Factor 2: degree of slope) and parental size measurements (female and male flipper length, bill depth, bill length) best predicted variation in nest size, egg size, hatching date and hatching success. Subcolony was introduced as a random factor. Degrees of freedom (df) are calculated with the Satterthwaite method and fixed effects are Type III tests.

[Resultados de los análisis GLIMM y GLIMMIX en los cuales las características de la subcolonia (Factor 1: grado de aislamiento; Factor 2: pendiente), y las medidas de los adultos (longitud de la aleta, longitud y altura del pico, tanto de machos como de hembras) mejor predicen la variación del tamaño del nido, tamaño del huevo, fecha de eclosión y el éxito reproductor. La subcolonia fue introducida como un factor aleatorio. Los grados de libertad (df) fueron calculados con el método Satterthwaite y los efectos fijos fueron de Tipo III.]

	Explanatory term [Términos explicativos]	Estimate [Estima]	df	F	P
Nest size					
[Tamaño del nido]	Factor 1	4.06	1,18.8	5.27	0.033
	Factor 2	-8.27	1,18.8	21.90	< 0.001
Egg size					
[Tamaño de huevo]	Factor 2	-1.02	1,211	4.16	0.043
Female flipper					
[Aleta de la hembra]	0.20	1,211	5.20	0.023	
Hatching date					
[Fecha de eclosión]	Factor 1	2.22	1,16.9	5.29	0.034
Hatching success					
[Éxito de eclosión]	Factor 1	-1.32	1,20	4.90	0.038

$F_{1,203} = 9.53$, $P = 0.0023$), which was not the case for bill length (GLMM: estimate = -0.034, $F_{1,203} = 0.23$, $P = 0.63$) or flipper length (GLMM: estimate = -0.081, $F_{1,203} = 1.37$, $P = 0.24$).

DISCUSSION

Subcolonies in penguins vary in size and in reproductive success, and several studies explored the relationship between both. Although penguins in large subcolonies generally showed better reproductive performance (Tenaza, 1971; Davis, 1982; Robertson, 1986; Young, 1994), such relationship was not found in some studies (Hunter, 1991; Emslie *et al.*, 1995). Other physical subcolony characteristics, which may or may not, be related to subcolony size, could explain additional variation in breeding performance among subcolonies. We found that subcolonies markedly differed in their degree of isolation and slope (Table 1). While subcolony isolation (Factor 1) was not correlated with subcolony slope (Factor 2, orthogonal factors), small subcolonies were those containing the largest slopes, but on the other hand also tended to be those that were most isolated (Table 1). Therefore, subcolony size is not the only responsible for all environmental variation among subcolonies in chinstrap penguins, although it appears that size is inherently related to the slope and isolation of the subcolony (Table 1). This could be an explanation for the observed inconsistent results with respect to effect of subcolony size on breeding success in different studies of penguins (Barbosa *et al.*, 1997, and references therein).

It is believed that the results with respect to breeding performance are conservative, because selection was made of active nests with the modal clutch size of 2 eggs at the middle of incubation. At that time, many nests had already lost one egg or their complete clutch. Since individuals of lower quality likely had a higher probability of losing their breeding at-

tempt soon after clutch completion, the real relationships between subcolony characteristics and breeding performance were possibly larger than the effects found in this study.

Results show that males with less bill depth were found in more sloped subcolonies. Bill size (depth and length) has been proposed to be related to adult age in Chinstrap Penguins (Mínguez *et al.*, 1998). Yearling penguins have smaller bills than breeding adults, whereas the size of their flippers shows no differences from breeding adults (Mínguez *et al.*, 1998). In addition, penguins with less bill depths occupy peripheral nest sites compared to pairs breeding in central sites in the same subcolony. Because this difference was found in males and females, less bill depth at peripheral sites was suggested to be rather an age related effect, than an effect of intrasexual competition for nest sites (Mínguez *et al.*, 2001). In the present study, bill depth between males and females of the same pair was positively related, which was not the case for bill length or flipper length. So, if bill depth in breeding adults were a sign of age, this correlation would suggest that members of the same pair were of similar age, and that young pairs occupied more sloped subcolonies. A possible explanation is that younger individuals arrive later at the rookery, such as occurs in adélie penguins *Pygoscelis adeliae*, and thereby older and more experienced individuals would already have occupied flat and large subcolonies (Williams, 1995). Further research is necessary to clarify the relationship between bill depth and age in penguins.

Furthermore, more sloped subcolonies also contained smaller eggs. It is well known that egg size has a positive effect on early growth and survival in many bird species (*e.g.* Smith *et al.*, 1998; Styrsky *et al.*, 1999; Hipfner, 2000) and also in chinstrap penguins (Belliere *et al.*, 1999). In some species, female age, next to body size and environmental conditions, explained additional variation in egg size (Hipfner *et al.*, 1997; Ratcliffe *et al.*, 1998; Parish *et al.*, 2001). If younger penguin pairs occupied

more sloped subcolonies, this could be a plausible explanation for the result that more sloped subcolonies also had smaller eggs.

On the other hand, isolation of the subcolony was the other factor explaining some of the variation in reproductive performance of penguins. More isolated subcolonies reproduced later and showed a lower hatching success, both reliable indicators of parental quality and breeding success in chinstrap penguins (Viñuela *et al.*, 1996; Moreno *et al.*, 1997). Although no parental body size variables were retained in the model explaining variation in hatching date or hatching success (Table 2), the degree of isolation of the subcolony did predict male bill length. However, up to date it is not clear if male bill length may indicate individual quality.

Nest size in penguins has been suggested to be an indicator of parental quality because stone collection and theft of nest material is a costly behaviour and breeding success in large nests was higher (Moreno *et al.*, 1995; Fargallo *et al.*, 2001). Given that males are more active than females collecting stones and defending the nest (Moreno *et al.*, 1995), nest building in the chinstrap penguin could also fit into sexual selection, based on the good parent process (Soler *et al.*, 1998; Fargallo *et al.*, 2001; Fargallo *et al.*, 2004). With respect to the present study, where individuals of more sloped and isolated subcolonies showed lower breeding performance in terms of egg size and hatching date/success respectively, it was expected that these subcolonies were comprised of smaller nests than central or flat subcolonies. Accordingly, a negative relationship existed between the subcolony slope (Factor 2) and average nest size of the subcolony (Table 2, Fig. 2). The main function of stone accumulation in a nest however is to prevent nest flooding under unfavourable weather conditions (Fargallo *et al.*, 2001) and is less problematic in the prevention of nest flooding on sloped rather than on flat ground. Furthermore, for obvious reasons, it is also easier to accumulate stones

for a nest on flat than on sloped ground, and then, smaller nests in sloped subcolonies can also be expected as a result of these physical subcolony characteristics, rather than a result of lower quality individuals breeding in more sloped subcolonies. An experimental approach would be useful to disentangle the effect of these possible factors on nest size in more sloped subcolonies. Furthermore, more isolated subcolonies that were occupied by individuals of lower parental quality (hatching success, hatching date), contained larger nests (Table 2, Fig. 2), which is in contrast with the expected relationship between nest size and parental quality. Nest size in general may be an honest signal of parental quality if the availability of nest materials and the pressure of theft are similar for different breeding pairs (Fargallo *et al.*, 2001). However, theft pressure has been shown to be lower and the availability of nest material to be larger in small compared to large subcolonies (Carrascal *et al.*, 1995). If additionally, the distance to neighbouring subcolonies is very large and the number of neighbours low, it is likely that the availability of nest materials will be larger and competition and theft pressure will be substantially lower for isolated than for central subcolonies. Therefore, it is possible that the larger nest size in isolated subcolonies is merely the consequence of these physical environmental characteristics (Carrascal *et al.*, 1995). Hence, differences in nest size among subcolonies do not necessarily reflect differences in parental quality, since physical environmental variables may alter the relationship between nest building effort and nest size.

In conclusion, this study indicates that subcolony slope and isolation, rather than just subcolony size, affect breeding success of chinstrap penguins. These results also indicate that nest size may act as an indicator of individual quality in chinstrap penguins (Fargallo *et al.*, 2001) only when compared within the same subcolony, or when the effect of subcolony is controlled for.

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