

## ORIGINAL PAPER

J. Moreno · J. Bustamante · J. Viñuela

**Nest maintenance and stone theft in the Chinstrap penguin (*Pygoscelis antarctica*)****1. Sex roles and effects on fitness**

Received: 21 November 1994/Accepted: 27 February 1995

**Abstract** Chinstrap penguins, *Pygoscelis antarctica*, after being relieved from incubation, collect stones from the ground or steal them from other nests and incorporate them into their own nests. The variation in stone-collecting behaviour after incubation reliefs, nest defence intensity and nest weights were measured in a sample of 100 nests in a large subcolony sited in the Vapour Col Chinstrap penguin colony on Deception Island, South Shetland Islands. Males collected more and larger stones, stole more stones and were more aggressive in nest defence towards potential thieves than females. Females suffered stone theft to a greater degree than males. Nests changed in weight during a period of 20 days. Initial nest size was negatively correlated with change in nest weight. The intensity of stone collection and theft by males was positively correlated with the increase in nest weight and with the final nest weight attained, while nest defence intensity by males and females was positively correlated with initial and final nest weight. Flooding after a snow storm affected 31% of nests and caused the loss of up to 14% of eggs/hatchlings. Flooded nests were significantly smaller than non-flooded nests. Results indicate that nest maintenance behaviour and stone theft in Chinstrap penguins serve to improve nest quality and thus enhance reproductive success.

**Introduction**

Nest maintenance behaviour is vital in the reproduction of birds, since it affects the environment to which

eggs and young altricial chicks will be exposed (Collias and Collias 1984). Pygoscelid penguins accumulate stones in scrapes in the ground to form a nest (Müller-Schwarze 1984). Nests can be variable in size (Bagshawe 1938; Müller-Schwarze 1984), possibly as a function of parental quality. In pygoscelid penguins, individuals relieved from incubation/brooding duties collect stones from the ground or steal them from other nests and deliver them to their mates at the nest (Levick 1915; Bagshawe 1938; Sapin-Jaloustre and Bourlière 1951; Sladen 1958; Tenaza 1971; Ainley 1975; Spurr 1975; Yeates 1975). These collecting trips often involve running the gauntlet through neighbouring territories. Nest defence against conspecifics during incubation/brooding is vigorous and directed against potential thieves (Bagshawe 1938; Ainley et al. 1983). Nest building may reduce the risk of nest flooding by melt-water after snowstorms (Müller-Schwarze 1984), but this effect has not yet been clearly proven. Also, the contribution of stone addition during incubation to penguin nest maintenance and improvement has never been quantitatively demonstrated. Alternatively, adding stones during nest reliefs may strengthen pair bonds (Roberts 1940), or serve individuals to advertise to their mates their vigour or aggressiveness through active nest maintenance. Information about body condition may be valuable in the context of nest relief coordination, which is of great importance in determining reproductive success in Adélie penguins, *Pygoscelis adeliae* (Davis 1982).

Theft occurs routinely as a form of stone collection in pygoscelid penguins (Levick 1915; Bagshawe 1938). Theft of nest materials can be considered as a form of nest construction or maintenance alternative to the collection of materials not included in nests and is generally considered as a cost of coloniality in birds (Collias and Collias 1984; Wittenberger and Hunt 1985). Theft of nest materials has been reported as frequent in many colonial species (e.g. cormorants, Williams 1942; frigate birds, Nelson 1975; gannets,

J. Moreno (✉) · J. Viñuela  
Museo Nacional de Ciencias Naturales-CSIC,  
J. Gutiérrez Abascal 2,  
E-28006 Madrid, Spain

J. Bustamante  
Estación Biológica de Doñana-CSIC, Paseo M<sup>a</sup> Luisa s.n.,  
E-41013 Sevilla, Spain

Nelson 1978; storks, Pomeroy 1978; herons, Lowe 1954; Siegfried 1972; swans, Frith 1979; gulls, Cullen 1957; Burger 1974; swallows, Emlen 1952; Hoogland and Sherman 1976; weavers, Crook 1964; Collias and Collias 1970; starlings, Rowley 1976; oropendolas, Skutch 1976; corvids, Coombs 1960; Balda and Bate-man 1972). Theft should occur when materials stolen from other nests are easier to obtain or of better quality than materials collected outside the colony (Burger 1974; Schleicher et al. 1993).

The roles of the sexes in nest defence are different in many bird species (Montgomerie and Weatherhead 1988; Breitwisch 1988), as they are in the context of nest building (Collias and Collias 1984). Thus we may expect sex-related differences in nest maintenance and defence in penguins (Spurr 1974; Viñuela et al. 1995). Given that there is active defence of the nest by owners, birds engaging in theft must gain some benefit in terms of nest quality to offset the risk of aggression. We can hypothesise that nest size should have a decelerating positive effect on reproductive success. Stone gathering and theft should be more important for pairs with nests smaller than the optimum for reproduction, while pairs with large nests should invest their effort in nest defence more than in nest improvement.

In the present study we investigate the sources of variation in stone collection, theft, nest defence and nest weight, focussing on sex differences. We also explore the importance of nest quality for reproductive success from incubation until chicks attain homeothermy. In a companion paper, (Carrascal et al. 1995) we explore the implications of subcolony size for robbing pressure as a potential cost of coloniality.

## Materials and methods

The study was conducted at the Vapour Col Chinstrap penguin colony (20,000 breeding pairs) on Deception Island, South Shetlands (63°00'S, 60°40'W), during the austral summer of 1993/1994. At the beginning of the study (4–8 December), we selected 100 nests scattered in a large subcolony (1,000 nests) and marked them with a wooden, numbered stick. Subcolonies are distinct dense aggregations of nests separated from each other by ground not used for nesting. As we were not specifically interested in the effect of nest position, we included the same number of peripheral (located in the first or second external row of the subcolony) and central nests (more than two rows deep inside the subcolony), and deliberately selected obviously large and small nests in both categories to include the whole range of variation in nest size independently of nest position. This non-random sampling method did not lead to a bimodal distribution of nest weights, but it does not allow us to compare nests according to nest position. Five nests contained one egg and the rest two eggs.

In these nests, one of the authors (JM) counted and weighed the stones longer than 1 cm on their major axis, at the beginning of the study (4–8 December). These stones were classified as medium (1–5 cm) or large (> 5 cm). Stones were carefully replaced and rearranged after weighing. Eggs were kept in a warm bag during the weighing procedure, which rarely took more than 5 min. No bird deserted due to weighing of nest stones. The first 30 nests sampled were not weighed at the beginning due to a misunderstanding, but

the stones were counted. All nests were again weighed after peak hatching (24–28 December). The interval between the two weighings was 20 (SD = 2.4) days, spanning a major part of the incubation period. On this occasion, we both weighed and counted the number of stones in the initially unweighed 30 nests. The initial weight of these nests was derived from a multiple linear regression of weight on number of large and medium stones: weight (g) = 287.97 + 8.53 (no. medium stones) + 168.05 (no. large stones),  $F_{1,98} = 484.32$ ,  $P < 0.001$ ,  $r^2 = 0.91$ .

Both members of the nest-owning pairs were banded with standard metal flipper bands (Lambournes); bill length and bill height at the nares were measured at the same time. Measurements were always taken by the same observer. To sex the penguins we used the discriminant function:

$$Z = 0.409 (\text{bill length}) + 4.113 (\text{bill height}),$$

derived for chinstrap penguins by Amat et al. (1993). Values of  $Z$  greater than 99.77 were assigned to males. This function correctly classifies 95% of individuals (Amat et al. 1993). In 15 pairs, the discriminant function assigned both members to the same sex. We did not use data for these pairs when analysing differences between sexes.

We followed opportunistically the activity of banded individuals (44 males and 50 females) during the first 30 min after being relieved by their mates from incubation, and recorded the following data: number of small (< 1 cm), medium and large stones delivered to the nest, number of stones of different size categories collected from less than 1 m, 1–3 m and more than 3 m from the nest, the number of unsuccessful theft attempts (UTA), the number of stones stolen from other nests (STA), the number of stones collected at temporarily unoccupied nests owned by failed breeders (CUN) and the total number of stones delivered at the nest (CTOT). For 22 birds, we collected data for two different incubation reliefs. All observations were made prior to hatching. On 35 occasions we noted the collecting behaviour for the whole relief period until the bird left for the sea. We also recorded the total relief duration of 52 individuals without observing their behaviour. To detect possible non-random selection with respect to sex of theft victims, we sexed the victims of 57 successful thefts by focal individuals and their nearest neighbour while looking away from the sea. No selection would imply a similar distribution of sexes in the victims and their neighbours.

To detect if relief period duration and stone collecting can be used as an estimate of the condition of the relieved individual, we weighed 13 males and 18 females with a Pesola spring balance when they left the colony for the sea. For 9 other males and 10 other females, we recorded their weights after the 30-min observation period and before they left the subcolony. The hatching date of the first chick to hatch in the 100 nests was recorded, as well as the number of chicks surviving 15 days after hatching. Chinstrap penguin chicks attain homeothermy at 15 days of age (Taylor 1985). A severe snow storm occurred 29–30 December, when most chicks in the colony had recently hatched. The state of nests and the egg/chick mortality were noted on 31 December. We considered that nests were drenched when nest contents were in contact with water.

According to our observations, intraspecific aggression in colonies during incubation is mostly associated with defence of nests against potential thieves (Viñuela et al. 1995). The defence intensity (DI) of banded individuals was measured by presenting a human fist for 30 s at 10 cm from the head of the nest occupant and counting the number of pecks directed at it. To check if nest defence against human observers reflects defence against stone theft, we performed an experiment in another subcolony. We selected 14 nests separated by more than 2 nests along the axis of 1 subcolony. Half of the nests were subjected to normal defence tests as above, while the other half were subjected to defence tests while removing five stones from the nest in full view of the nest occupant. Each nest occupant was subjected to three defence tests separated by more than 15 min. The aim was to detect if stone removal affected DI level and the degree of attenuation of DI with experience. If DI is related to a response

against theft (and not to predators or simply to intrusion), we should expect a greater response and a reduced attenuation in nests subjected to stone removal.

We performed an experiment in another subcolony to quantify the turn-over rate of stones in large and small nests. We placed ten stones of average size marked with yellow paint on top of ten central nests weighing less than 2 kg and in ten central nests weighing more than 4 kg. After 11 days, we counted the number of painted stones remaining and weighed the nests again.

Parametric analyses were employed, using the square root transformation for rates of behaviour and the cubic root transformation for nest weight. We have performed ANCOVAs and two-way ANOVAs with PROC ANOVA for balanced designs and PROC GLM with type III sums of squares for unbalanced designs. Means are presented with SE. All tests are two-tailed. Probabilities smaller than 5% are termed significant.

## Results

### Variation in stone collection

We selected three behavioural measures of stone gathering and stone theft effort, namely the total number of stones carried (CTOT), the total number carried minus the stones gathered at temporarily unoccupied nests owned by failed breeders (CTOT - CUN) and the sum of unsuccessful and successful theft attempts (UTA + STA). The variable CUN showed very high random variation introduced by the presence of temporarily undefended nests in the vicinity of the focal nest at the time of observations, which led to very high rates of stone collection, as stones in these nests were removed by recently relieved neighbours immediately after their owners left the colony (see also Ainley 1975). Thus, the percentage of stones collected at these nests (of the total) was very variable for males and females (males:  $22.0 \pm 6.1\%$ ,  $n = 36$ ; females:  $18.8 \pm 5.5\%$ ,  $n = 39$ ) and did not differ between sexes ( $F_{1,73} = 0.328$ ,  $P = 0.569$ ). These three measures represent three different aspects of stone-gathering behaviour. The first is a general measure of stone gathering, the second (hereafter called partial collection) excludes the large random variation introduced by the variable CUN, while the third measure represents the effort deployed in theft.

The total amount of stones collected/stolen during a complete relief period can be estimated from the amount collected/stolen in the first 30-min after relief (linear regressions: CTOT:  $F_{1,33} = 95.4$ ,  $P < 0.001$ ,  $r^2 = 74.9$ ; (CTOT-CUN):  $F_{1,33} = 77.9$ ,  $P < 0.001$ ,  $r^2 = 70.9$ ; (UTA + STA):  $F_{1,33} = 25.3$ ,  $P < 0.001$ ,  $r^2 = 44.1$ ). We will hereafter use the data for 30-min observation periods. To detect if individuals were consistent in their collecting/theft behaviour between observations, we performed ANCOVAs with sex as the factor and the second observation as covariate. In these analyses, only theft attempt frequency was significantly consistent between observations [CTOT: sex:  $F_{1,17} = 0.10$ ,  $P = 0.76$ , observation:  $F_{1,17} = 1.69$ ,

$P = 0.21$ ; (CTOT - CUN): sex:  $F_{1,15} = 1.20$ ,  $P = 0.29$ , observation:  $F_{1,15} = 2.93$ ,  $P = 0.107$ ; (UTA + STA): sex:  $F_{1,15} = 4.60$ ,  $P = 0.049$ , observation:  $F_{1,15} = 34.12$ ,  $P < 0.001$ ]. Males collected significantly more medium and large stones than females (Table 1), while there was a marginally significant difference with respect to transport distance (Table 1). The sexes did not differ with respect to total stone collection, but males had a significantly higher theft intensity than females (Table 1).

### Stone collecting and body condition

The duration of relief periods (from relief to departure for the sea) was on average  $86 \pm 10$  min (median = 50 min, range = 9–420 min,  $n = 87$ ). There was a significant positive correlation between relief duration and body weight at departure (ANCOVA: sex:  $F_{1,36} = 0.03$ ,  $P = 0.86$ ; weight:  $F_{1,36} = 6.89$ ,  $r = 0.488$ ,  $P = 0.013$ ). However, stone collection intensity was not related to weight at departure (CTOT: ANCOVA, sex,  $F_{1,49} = 1.27$ ,  $P = 0.26$ ; weight,  $F_{1,49} = 0.67$ ,  $P = 0.41$ ; (CTOT - CUN): ANCOVA, sex  $F_{1,49} = 0.29$ ,  $P = 0.60$ ; weight,  $F_{1,49} = 0.21$ ,  $P = 0.65$ ; (UTA + STA): ANCOVA, sex  $F_{1,49} = 10.35$ ,  $P = 0.002$ ; weight:  $F_{1,49} = 0.11$ ,  $P = 0.74$ ).

An indication of breeding experience and parental quality may be given by the body weights attained when relieved. The more experienced or successful breeders may coordinate better their nest reliefs during incubation (Davis 1982), so being able to keep more of their reserves. Females of pairs having large nests left for the sea with greater weights (correlation nest weight-female weight:  $r_{25} = 0.59$ ,  $P = 0.001$ ). This is not so for males ( $r_{19} = 0.22$ ,  $P = 0.33$ ). Thus, males that are able to reduce the incubation periods of their mates by returning more rapidly from the sea, are also those capable of building and defending large nests.

### Variation in nest defence intensity

Individuals subjected to stone theft during DI tests responded more vigorously than those that experienced normal DI tests (Table 2): this was so for the first, second and third consecutive tests (Table 2). Individuals subjected to normal DI tests showed a diminished response during consecutive tests, but this was not the case for individuals that experienced theft during tests (ANOVA for repeated measures with test order and treatment: test:  $F_{2,23} = 0.90$ ,  $P = 0.42$ ; test  $\times$  treatment:  $F_{2,23} = 5.84$ ,  $P = 0.009$ ; polynomial contrast for linear tendencies: mean of treatments  $F_{1,24} = 0.51$ ,  $P = 0.48$ ; treatment  $F_{1,24} = 9.65$ ,  $P = 0.005$ ; Table 2). We concluded that defence intensity was affected by stone theft and that our DI tests reflected responses to stone removal.

**Table 1** Differences between sexes in frequencies ( $\bar{x} \pm \text{SE}$ ) for different aspects of stone gathering in Chinstrap penguins (*CTOT* total stone collection, *CTOT* – *CUN* total stone collection except stones collected at temporarily unoccupied nests, *UTA* + *STA* successful and unsuccessful theft attempts)

	Males (44) <sup>a</sup>	Females (50)	<i>F</i>	<i>P</i>
Stone size				
Small stones	8.1 ± 1.8	7.1 ± 2.0	1.04	0.310
Medium stones	2.1 ± 0.6	0.7 ± 0.2	5.82	0.018
Large stones	1.0 ± 0.3	0.2 ± 0.1	9.81	0.002
Collection distance				
From < 1m	5.2 ± 1.4	5.1 ± 1.8	0.68	0.419
From 1–3 m	4.4 ± 1.4	1.5 ± 0.5	3.74	0.056
From > 3 m	1.6 ± 0.5	0.7 ± 0.3	3.54	0.063
Stones carried				
<i>CTOT</i>	11.2 ± 2.1	7.2 ± 2.0	3.60	0.061
Partial stone collection ( <i>CTOT</i> – <i>CUN</i> )	5.8 ± 1.1	4.5 ± 1.2	1.83	0.180
Theft attempts ( <i>UTA</i> + <i>STA</i> )	3.1 ± 0.8	0.7 ± 0.3	13.21	0.001

<sup>a</sup> Sample sizes in parentheses are number of individuals observed

**Table 2** Differences in defence intensity (*DI*) ( $\bar{x} \pm \text{SE}$ ) of incubating individuals subjected to normal *DI* tests and to tests in which stones were visibly removed by the observer

	Control	Stones removed	t-tests	
	(7) <sup>a</sup>	(7)	t	<i>P</i>
First test	20.85 ± 4.13	29.92 ± 2.22	2.21	0.036
Second test	14.77 ± 2.90	33.23 ± 2.21	4.49	< 0.001
Third test	14.54 ± 2.82	35.23 ± 2.46	4.79	< 0.001
Mean	16.72 ± 3.16	32.79 ± 1.74	4.06	< 0.001

<sup>a</sup> Sample sizes in parentheses are number of individuals observed

Males showed a significantly greater *DI* than females ( $19.13 \pm 1.24$  pecks vs.  $12.01 \pm 1.07$  pecks,  $F_{1,168} = 18.83$ ,  $P < 0.001$ ). The reduced response of females could make them more susceptible to being robbed while incubating than males. In 57 observations of successful theft we sexed the robbed individuals from bill measurements as females in 38 cases and as males in 19 cases. The nearest neighbours were females in 23 cases and males in 34 cases. The two distributions of sexes were significantly different ( $\chi^2_1 = 17.7$ ,  $P < 0.001$ ). Females were apparently more prone to being robbed than males, as would be predicted from their lower *DI*. Larger females were more vigorous in their defence (correlation of *Z* with *DI*:  $r_{81} = 0.25$ ,  $P = 0.02$ ), while this was not so for males ( $r_{83} = 0.06$ ,  $P = 0.60$ ).

#### Variation in nest weight

Nests weighed on average  $3358 \pm 205$  g (range = 300–10691,  $n = 100$ ) and contained on average  $247 \pm 12$  stones larger than 1 cm (range = 36–641,  $n = 100$ ). During a period of 20 days (roughly 66% of

the 30-day incubation period and 44% of the 45-day incubation and brooding period), the increase in nest weight was on average  $172 \pm 139$  g (range = –7341 to +3750,  $n = 98$ ; two nests that were lost before the final weighing were not included). The change in nest weight was not significant for the whole sample of nests (repeated measures ANOVA:  $F_{1,96} = 1.53$ ,  $P = 0.22$ ). Although the average change in weight was not different from zero, approximately half of the nests (57.1%) gained weight through collection and theft, while the other half (41.8%) lost weight through theft (the distribution was not significantly different from 50:50%). The proportional weight change of nests was on average  $20 \pm 6\%$  (range = –69% to +300%,  $n = 98$ ). However, the proportional weight increments were significantly larger than the proportional weight decrements ( $48.9 \pm 7.9\%$  vs.  $19.6 \pm 2.1\%$ ;  $F_{1,96} = 8.42$ ,  $P = 0.005$ ). Nest increments were larger than losses probably due to stones collected from the ground and not stolen. The initial nest weight was negatively correlated with change in weight ( $r_{96} = -0.31$ ,  $P = 0.002$ ). Thus, initially large nests were the ones that increased the least in weight.

**Table 3** Correlations of initial and final nest weight and change in nest weight with stone-collecting behaviour and defence intensity of males and females

	Initial nest weight		Final nest weight		Change in nest weight		df
	<i>r</i>	<i>P</i>	<i>r</i>	<i>P</i>	<i>r</i>	<i>P</i>	
Stones carried							
CTOT <sup>a</sup> males	-0.006	0.97	0.134	0.39	0.262	0.09	41
CTOT females	-0.037	0.80	-0.108	0.46	-0.073	0.62	46
Partial stone collection							
(CTOT-CUN) males	-0.001	0.99	0.166	0.29	0.382	0.01	41
(CTOT-CUN) females	-0.096	0.51	-0.218	0.14	-0.129	0.38	46
Theft attempts							
(UTA + STA) males	0.159	0.31	0.293	0.06	0.380	0.01	41
(UTA + STA) females	-0.342	0.02	-0.331	0.02	0.059	0.69	46
Defence intensity							
DI males	0.312	0.004	0.322	0.003	0.005	0.97	82
DI females	0.251	0.02	0.291	0.008	0.090	0.42	80

<sup>a</sup>See Table 1 for definitions

### Nest weight and nest maintenance

The two main forms of maintaining nests in the presence of theft are the collecting of new stones and the defence of ones already in the nest. Initial and final nest weights showed no significant relationship with any stone-collecting/theft variable for males, although theft frequency vs. final nest weight was nearly significant (Table 3). However, initial and final nest weights were negatively correlated with theft intensity among females (Table 3). There were significant positive relationships between stone gathering and stone theft by males and the increment in nest weight (Table 3). DI of males and females was significantly related to initial and final nest weight (Table 3). There was no effect of DI of either males or females on change in nest weight (Table 3).

### Nest weight and stone turn-over

Large and small nests in this experiment were significantly different ( $7,850 \pm 359$  g vs.  $1,425 \pm 136$  g;  $F_{1,18} = 280$ ,  $P < 0.001$ ). There was no difference in the number of painted stones remaining in large and small nests after 11 days ( $7.1 \pm 0.8$  vs.  $6.9 \pm 0.8$ ;  $F_{1,18} = 0.04$ ,  $P = 0.85$ ). Thus, small nests were not subjected to a greater theft exposure than large nests. Assuming that painted stones were as attractive as non-painted stones for the penguins, the proportions of stolen stones in large and small nests would imply significantly different total weights of stolen stones in large and small nests (proportion of painted stones stolen  $\times$  initial nest weight:  $2,325 \pm 635$  g vs.  $394 \pm 73$  g;  $F_{1,18} = 9.12$ ,  $P = 0.007$ ). Large nests also showed the tendency of being the ones increasing the least in weight in this sample, although the difference was not significant

( $-120 \pm 313$  g vs.  $805 \pm 338$  g;  $F_{1,18} = 4$ ,  $P = 0.06$ ). The turn-over rate of 30% of stones in 11 days would mean an almost complete turn-over of stones in nests during the 1-month incubation period.

### Nest weight and reproductive success

The impact of the snow storm from 29–30 December was obvious: 30 nests were flooded by melt-water on 31 December. In seven of these, there was one dead or missing chick. The four dead chicks still remaining in the nests were completely wet. In 11 other nests, which were not as wet, there were 4 chicks and 7 eggs missing. Four other nests with two eggs/chicks had been deserted and contained no stones. Thus 7–26 eggs/chicks (considering only visibly flooded nests or the whole sample of 22 nests possibly affected by the storm) were lost after this critical event; this amounts to 4–14% of eggs/chicks in 7–23% of the nests (four nests had been lost before the storm). Flooded nests were significantly smaller than the rest (final weights:  $2,788 \pm 394$  g,  $n = 30$  vs.  $3,984 \pm 225$  g,  $n = 64$ ;  $F_{1,92} = 12$ ,  $P < 0.001$ ). However, nests that were visibly flooded on 31 December were not less successful than the others, as estimated by the number of chicks raised until the age of 15 days ( $1.52 \pm 0.12$  vs.  $1.40 \pm 0.10$  chicks, Kolmogorov-Smirnov test:  $\chi^2_2 = 0.75$ ,  $P > 0.50$ ). This probably means that mortality factors other than that single storm operated to determine reproductive success.

The number of young surviving until 15 days of age (0, 1 or 2) was associated with initial and final nest weight. Pairs with larger nests had greater reproductive success (Table 4). Also, the number of eggs/chicks lost was related to nest weight ( $F_{2,97} = 10.61$ ,  $P < 0.001$ ). The change in weight of nests did not differ for pairs

**Table 4** Nest weight (g;  $\bar{x} \pm \text{SE}$ ) at the beginning and end of the study as a function of the numbers of chicks raised to age 15 days

	No chick	One chick	Two chicks	$F_{2,92}$	$P$
Initial nest weight	2288 $\pm$ 416 (18) <sup>b</sup>	2650 $\pm$ 330 (26)	4003 $\pm$ 277 (51)	10.23	< 0.001
Final nest weight	2581 $\pm$ 405 (18)	2813 $\pm$ 346 (26)	4049 $\pm$ 282 (51)	7.57	< 0.001

<sup>a</sup>Means under the same line are not significantly different (Scheffe tests)

<sup>b</sup>Number of nests

raising 0, 1 or 2 chicks to the age of 15 days ( $F_{2,95} = 0.75$ ,  $P = 0.47$ ).

## Discussion

Observers of pygoscelid penguins have noted the thievery of nest stones that goes on continuously during the early breeding stages (Sapin-Jaloustre and Bourlière 1951; Tenaza 1971; Ainley 1975; Spurr 1975; Yeates 1975). The most detailed account of this behaviour in Gentoo *Pygoscelis papua* and Chinstrap penguins was completed by Bagshawe (1938). He summed up his delightful descriptions of penguin thievery by observing: "Thieving is part of a penguin's nature and is so universally indulged in that it may be regarded as a normal habit rather than a sin". However, most reports have only noted the behaviour in passing, in spite of the considerable time and energy that breeding penguins devote to it. Only Bagshawe (1938) associated the huge individual variation in nest quality with the tendency to collect and steal stones from other nests in pygoscelid penguins. However, the connection between the activity and its proposed adaptive result, i.e. improvement of nest quality, has heretofore never been quantitatively shown in pygoscelids.

Results from this study showed that stone-collecting behaviour after nest reliefs varied greatly among incubating Chinstrap penguins. Males collected larger stones, collected stones further away from the nest and stole more than females. Stone gathering by males, especially theft, had a positive effect on change in nest weight throughout the incubation period. It has been proposed by several authors that theft may be prevalent when it takes less time to steal material from conspecifics than to gather it anew (Cullen 1957; Collias and Collias 1978; Schleicher et al. 1993), or when the material in other nests is of better quality or easier to gather than that available around the nests (Burger 1974). In the companion paper (Carrascal et al. 1995), we show that stolen stones are significantly larger than those collected and that individuals breeding in large aggregations are forced by collection costs to steal stones.

We observed that nests could be maintained or improved through collection of new stones and/or through defence of the stones already present. Males are more vigorous in defending nests against potential thieves than females. Spurr (1974) obtained a similar result for Adélie penguins during the incubation phase. Females, on the other hand, lose more stones through theft while incubating than males. Female size offsets to a certain degree the difference between sexes in aggressiveness. A plausible origin for these intersexual differences is the possibly greater involvement of males in nest construction. Aggressive males and females have larger nests, but do not significantly augment them throughout incubation. The fact of having built a large nest and the means to defend it may reduce the need to indulge in thievery. One has to bear in mind that stone gathering means running the gauntlet among crowded territories, being threatened by nest proprietors or incurring the wrath of recently relieved individuals (fights among Chinstrap penguins are frequently vicious and, on rare occasions, can lead to death, unpublished observations). Birds having large nests do not incorporate more stones through theft but experience the same turn-over rate of stones as do individuals having small nests, as shown in our experiment. This rate means an almost complete turn-over of stones in the nests through stealing throughout the incubation period.

The sum of the weights of all nests in the sample barely changes during the incubation period, but some nests gain weight at the expense of others. It is this variation between nests and their owners that is of biological importance and not the average nest weight change in the population. Theft intensity by males significantly affects weight change, while defence intensity by males is not involved in the increase in nest weight. Males that are efficient in collecting and stealing stones are those that, having initially small nests, can enlarge them with, on average, 50% of their bulk. However, this result is partly based on the unsuccessful nest defence of other nest owners, which lose, on average, 20% of their nests. Thus, nests that have not initially attained an optimum size can be built upon continuously through collecting/stealing by males, until the risk of nest flooding becomes insignificant.

Apparently, females with small nests indulge more in thievery, possibly due to the weak nest defence of their mates. The results show that some males can build large nests and defend them efficiently (probably the most dominant males), other males of intermediate dominance are able to improve nest quality through stone collection and theft, while subordinate males are neither able to defend their nest appropriately nor to collect enough stones to offset theft by neighbours.

There are frequent reports in the literature on Adélie penguins about the deleterious effects of thaw-water on reproductive success (e.g. Reid 1964; Yeates 1968; Müller-Schwarze 1984; but see Taylor 1962; Davis and McCaffrey 1986). However, Chinstrap penguins breed in areas having higher levels of precipitation and higher temperatures (maritime Antarctic) than the Adélie penguin breeding areas studied, and, accordingly, may be subjected to greater risks of nest flooding. Even if the probability of severe storms hitting during the critical period was low, their impact on reproductive success could be strong enough to select for active improvement of initially suboptimal nests. The importance of flooding may be greatest at the time of hatching, due to the size and thermoregulatory capacity of hatchlings. In our study, 14% of eggs/hatchlings in 23% of nests were lost after one storm hit a few days after peak hatching. Flooding occurred to some degree in 30% of the nests. Larger nests had a smaller risk of becoming flooded by melt-water as shown by the difference in size between drenched and dry nests in our sample. However, the number of chicks raised to homeothermic age did not differ among nests that were or were not visibly drenched on that occasion. Factors other than nest size may have affected hatching success (e.g. relief coordination by mates) and nestling survival (food delivery rates, antipredator defence) throughout the 45-day incubation/brooding period, thus blurring the effect of nest quality. Also, the possible costs to parents of keeping eggs and chicks warm in muddy and wet nests after the frequent rains and mild snowsqualls have not been measured, but could be significant. An indication of a long-term effect of nest quality is shown by the association of large nests with greater reproductive success at the time of chick thermal independence. However, nest size may be just another correlate of parental quality, contributing to breeding success together with foraging efficiency, coordination in nest reliefs, antipredator aggressiveness etc. There is some evidence that pairs with larger nests have a more coordinated incubation schedule as evidenced by female weight after fasting. However, the fact that larger nests are less prone to flooding suggests that the adaptive function of stone gathering is the improvement of the protective properties of nests.

An alternative function for stone gathering, i.e. that it serves to transfer information about the physical condition of the relieved individual to its mate, is not sup-

ported by our results. Relief period duration was positively related to weight after the incubation fast, but stone-gathering behaviour by relieved individuals did not show any relationship to weight. Thus, the duration of the relief periods could give information about the nutritional state of the relieved individual to its mate, while stone-gathering behaviour would not. The possibility that stone collection, as well as improving nest quality, also serves to reinforce pair bonds remains to be explored.

**Acknowledgements** This study was funded by the Spanish Antarctic Program, C.I.C.Y.T. (grant ANT91-1264). Transport to and from Deception Island was made on the ship "*Hespérides*", of the Spanish Navy. The study was located on the Spanish Army base "Gabriel de Castilla". We gratefully acknowledge the cooperation offered by all participants in the Spanish Antarctic campaign 1993/1994. David Ainley, Kate Lessells and several anonymous referees offered constructive criticisms on a previous version of the manuscript.

## References

- Ainley D (1975) Displays of Adélie penguins: a reinterpretation. In: Stonehouse B (ed) *Biology of penguins*. University Park Press, Baltimore, pp 503–534
- Ainley DG, Leresche RE, Sladen WJL (1983) *Breeding biology of the Adélie penguin*. University of California Press, Berkeley
- Amat JA, Viñuela J, Ferrer M (1993) Sexing Chinstrap penguins (*Pygoscelis antarctica*) by morphological measurements. *Colon Waterbirds* 16:213–215
- Bagshawe TW (1938) Notes on the habits of the gentoo and ringed or Antarctic penguins. *Trans Zool Soc London* XXIV:185–291
- Balda RP, Bateman GC (1972) The breeding biology of the pinion jay. *Living Bird* 11:5–42
- Breitwisch R (1988) Sex differences in defence of eggs and nestlings by northern mockingbirds *Mimus polyglottus*. *Anim Behav* 36:62–72
- Burger J (1974) Breeding adaptations of Franklin's gull (*Larus pipixcan*) to a marsh habitat. *Anim Behav* 22:521–567
- Carrascal LM, Moreno J, Amat JA (1995) Nest maintenance and stone theft in the Chinstrap penguin *Pygoscelis antarctica*. II. Effects of breeding group size. *Polar Biology* 15:541–546
- Collias EC, Collias NE (1970) The behaviour of the West African village weaverbird. *Ibis* 112:457–480
- Collias EC, Collias NE (1978) Nest building and nesting behaviour of the sociable weaver *Philetarius socius*. *Ibis* 120:1–15
- Collias EC, Collias NE (1984) *Nest building and bird behavior*. Princeton University Press, Princeton
- Coombs CJF (1960) Observations on the rook *Corvus frugilegus* in southwest Cornwall. *Ibis* 102:394–419
- Crook JH (1964) The evolution of social organization and visual communication in the weaver birds (Ploceinae). *Behaviour [Suppl]* 10:1–178
- Cullen E (1957) Adaptations in the kittiwake to cliff-nesting. *Ibis* 99:275–302
- Davis LS (1982) Timing of nest relief and its effect on breeding success in Adélie penguins (*Pygoscelis adeliae*). *Condor* 84:178–183
- Davis LS, McCaffrey FT (1986) Survival analysis of eggs and chicks of Adélie penguins (*Pygoscelis adeliae*). *Auk* 103:379–388
- Emlen JT (1952) Social behavior in nesting Cliff Swallows. *Condor* 54:177–199
- Frith HJ (1979) *Reader's Digest Complete Book of Australian Birds*. Reader's Digest, Sydney

- Hoogland JL, Sherman PW (1976) Advantages and disadvantages of bank swallow (*Riparia riparia*) coloniality. *Ecol Monogr* 46:33–58
- Levick GM (1915) Natural history of the Adélie penguin. British Museum (Natural History), London
- Lowe FA (1954) The herons. Collins, London
- Montgomerie RD, Weatherhead PJ (1988) Risks and rewards of nest defence by parent birds. *Q Rev Biol* 63:167–187
- Müller-Schwarze D (1984) The behavior of penguins. State University of New York Press, Albany
- Nelson JB (1975) The breeding biology of frigate birds – a comparative review. *Living Bird* 14:113–156
- Nelson JB (1978) The Sulidae: gannets and boobies. Oxford University Press, Oxford
- Pomeroy DE (1978) The biology of Marabou storks in Uganda. 2. Breeding biology and general review. *Ardea* 66:1–23
- Reid BE (1964) The Cape Hallett Adélie penguin rookery, its size, composition and structure. *Rec Dom Mus Wellington* 5:11–37
- Roberts BB (1940) The breeding behaviour of penguins with special reference to *Pygoscelis papua* (Forster). *Sci Rep Br Graham Land Exped 1934-7* 3:195–254
- Rowley I (1976) Cooperative breeding in Australian birds. In: Frith HJ, Calaby JH (eds) *Proc XVIth International Ornithological Congress*. Australian Academy of Sciences, Canberra, pp 657–666
- Sapin-Jaloustre J, Bourlière F (1951) Incubation et développement du poussin chez le Manchot Adélie *Pygoscelis adeliae*. *Alauda Rev Int Ornithd* 2:65–82
- Schleicher B, Valera F, Hoi H (1993) The conflict between nest guarding and mate guarding in penduline tits (*Remiz pendulinus*). *Ethology* 95:157–165
- Siegfried WR (1972) Breeding success and reproductive output of the cattle egret. *Ostrich* 43:43–55
- Skutch AF (1976) Parent birds and their young. University of Texas Press, Austin, Tex
- Sladen WJL (1958) The pygoscelid penguins. 1, 2. *Sci Rep Falkland Islands Dependency Surv* 17:1–97
- Spurr EB (1974) Individual differences in aggressiveness of Adélie penguins. *Anim Behav* 22:611–616
- Spurr EB (1975) Communication in the Adélie penguin. In: Stonehouse B (ed) *Biology of penguins*. University Park Press, Baltimore, pp 449–501
- Taylor JRE (1985) Ontogeny of thermoregulation and energy metabolism in pygoscelid penguin chicks. *J Comp Physiol B* 155:615–627
- Taylor RH (1962) The Adélie penguin *Pygoscelis adeliae* at Cape Royds. *Ibis* 104:176–204
- Tenaza R (1971) Behavior and nesting success relative to nest location in Adélie penguins (*Pygoscelis adeliae*). *Condor* 73:81–92
- Viñuela J, Amat JA, Ferrer M (1995) Nest defence of nesting Chinstrap penguins (*Pygoscelis antarctica*) against intruders. *Ethology* 99:323–331
- Williams L (1942) Display and sexual behavior of the Brandt cormorant. *Condor* 44:85–104
- Wittenberger JF, Hunt GL (1985) The adaptive significance of coloniality in birds. In: Farner DS, King JR (eds) *Avian biology*, vol VIII. Academic Press, New York, pp 1–78
- Yeates GW (1968) Studies on the Adélie penguin at Cape Royds 1964–65 and 1965–66. *NZJ Mar Freshwater Res* 2:472–496
- Yeates GW (1975) Microclimate, climate and breeding success in Antarctic penguins. In: Stonehouse B (ed) *Biology of penguins*. University Park Press, Baltimore, pp 397–409