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ORIGINAL PAPER

L.M. Carrascal · J. Moreno · J.A. Amat

Nest maintenance and stone theft in the Chinstrap penguin (*Pygoscelis antarctica*)

2. Effects of breeding group size

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Abstract The intensity of stone collection and stone theft by breeding Chinstrap penguins was measured, and estimations made of the number of stones per nest in large (> 400 nests) and small subcolonies (< 50 nests) in the large Vapour Col colony on Deception Island, South Shetland Islands. Stone availability was significantly higher both inside and outside small subcolonies. Penguins carried stones to the nest at the same rate in large and small subcolonies, but stole more intensively in large subcolonies. Stones obtained by theft were significantly larger than those collected elsewhere. When stone availability was increased experimentally, individuals of large subcolonies collected more intensively than control individuals in large and small subcolonies, and stole significantly less than control individuals in large subcolonies, and as much as individuals in small subcolonies. The greater theft pressure in large subcolonies was accompanied by more aggressive defence by nest owners and by reduced success in stealing. However, the reduced availability of stones on the ground near large subcolonies led to a significantly lower number of stones per nest than in small subcolonies. These results are interpreted in the light of the geometric effects of breeding group size (perimeter to surface ratio) on stone accessibility.

Introduction

Nest materials in penguin colonies may be in short supply or costly to obtain. As a result, competition for nest material may be a disadvantageous consequence of colonial breeding (Burger 1981; Wittenberger and Hunt 1985). If nest materials stolen from neighbouring nests are easier to obtain or of better quality than materials collected from the surroundings of colonies, theft may become a viable form of nest building and/or nest maintenance (Burger 1974; Schleicher et al. 1993). Although theft of nest materials has been documented in several avian groups (see Moreno et al. 1995), the adaptiveness of such thieves with respect to time/energy savings has seldom been quantified. Schleicher et al. (1993) showed that thieves spent less time stealing materials from unguarded nests than collectors did gathering them from the surroundings (in the penduline tit *Remiz pendulinus*). Also, if competition for nest materials through theft is to be considered as a cost of avian coloniality, a positive relationship of theft frequency with subcolony size has to be demonstrated, at least up to a threshold. Hoogland and Sherman (1976) noted that stealing was never observed in the smallest of three sand martin *Riparia riparia* colonies, and suggested an advantage regarding nest material retention to members of smaller colonies. However, there is, to our knowledge, no study showing that more frequent thievery of nest materials results in smaller nests.

Aggressive defence of nest materials (Balda and Bateman 1972) and the permanent presence of one pair member at the nest (Cullen 1957; Coombs 1960) are possible ways of coping with theft during nest building. Theft has been described mostly in unguarded nests at this stage (Cullen 1957; Balda and Bateman 1972; Hoogland and Sherman 1976; Pomeroy 1978; Schleicher et al. 1993). For this situation, Wittenberger and Hunt (1985) suggested that exposure to theft may depend on breeding date, with early breeders having a greater exposure and less opportunity to benefit from theft than late breeders. For the average individual, the chance of losing nest materials in a large colony would be balanced by the greater availability of pilferable material close to the nest. However, colony size may

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

J.A. Amat
Estación Biológica de Doñana-CSIC,
Paseo Mª Luisa S.N.,
E-41013 Sevilla, Spain

affect the availability of nest materials in the periphery of colonies through a different depletion due to the geometric effect of perimeter to area ratio of colonies (Tenaza 1971). The effects of colony size on availability of collectable nest materials in the periphery of colonies have to our knowledge, not been quantified in any avian species.

Pygoscelid penguins use stone mounds for nesting, a fact that may have encouraged coloniality in these species. In the Southern Ocean region, ice-free terrain with a good supply of stones for building nests is a limited resource. The theft of stones used as nest materials in pygoscelid penguins has been frequently reported (Levick 1915; Bagshawe 1938; Sapin-Jaloustre and Bourlière 1951; Sladen 1958; Penney 1968; Tenaza 1971; Ainley 1975; Spurr 1975; Yeates 1975; Moreno et al. 1995). Frequently, nests occupied by incubating individuals are subjected to pilfering of stones (Bagshawe 1938). In a companion paper (Moreno et al. 1995), we have shown that nest maintenance behaviour, including theft, is associated with improvements in nest size during the incubation phase in the Chinstrap penguin *Pygoscelis antarctica.* We have also shown that defence of nest stones by males is associated with larger nests, and that larger nests are less prone to being flooded by melt water. Finally, we have shown that pairs with larger nests are more successful in reproduction, although this difference could be affected by other correlates of parental quality. Chinstrap penguins breed within colonies in distinct dense aggregations of nests separated from each other by ground not used for nesting. These subcolonies can have from 5 to more than 1,000 nests. This huge range in breeding group size allows us to determine the repercussions of competition for nest materials and to ascertain the importance of this factor as a cost of colonial breeding. In the present paper, as a function of breeding group size, we (1) study the variation in nest size, (2) describe differences in stone collection with respect to the incidence of theft, (3) relate theft success to nest defence intensity, and (4) determine the impact of the availability of stones within and in the periphery of colonies.

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 December 1992. We selected subcolonies depending on the number of breeding pairs. We defined subcolonies as small (10–50 pairs) and large (> 400 pairs). The distance between the centres of consecutive nests (estimated with a tape measure) did not significantly differ between small and large subcolonies (small subcolonies: $\bar{x} = 70$ cm, SE = 1.33, $n = 90$; large subcolonies: $\bar{x} = 70.5$ cm, SE = 1.11, $n = 100$; $F_{1,188} = 0.226$, $P = 0.635$), so nest density was not related to subcolony size. We selected nests sequentially as multiples of five (large subcolonies) or three (small subcolonies) along transects initiated at the periphery of subcolonies (thus excluding peripheral nests). In each selected nest, one person (always the same researcher) counted directly the number of stones larger than 1 cm in diameter. From the nestcup of each nest, two handfuls of stones were removed and placed in a plastic bag, and then weighed and counted to measure the average weight of stones; the stones were subsequently returned to the nest and carefully rearranged. Only nests with two eggs were considered for treatment in this way.

Using a string we measured the number of stones > 1 cm diameter available between the studied nest and its nearest neighbour. The string was oriented towards the sea, and stones were counted in a belt of 1 m of length (defined by the string) and 5 cm of width on each side of the string. We also counted the number of stones in the periphery of the subcolony (from the subcolony edge to 5 m) using the same procedure carried out on measuring stone availability between nests. Samples were obtained by random sampling in the accessible subcolonies within the colony (five small and seven large subcolonies).

The behaviour of focal individual birds carrying stones to their nests was monitored continuously for periods of 15 mins; only birds that had been relieved of incubation actively collected stones (Moreno et al. 1995). Focal individuals were the first birds observed carrying stones to their nests after the observer arrived at the study subcolony. For each individual, we recorded the number of stones collected from the ground, those stolen from nests occupied by an incubating individual (successful theft attempts) or those pilfered from temporarily unoccupied nests owned by reproductively unsuccessful pairs, and also the number of unsuccessful theft attempts, the relative size of stones (small, score 1; medium, score 2; large, score 3; Moreno et al. 1995) and the distance from which stones were obtained (visually estimated in meters). From these variables we calculated two other outcomes: the percentage of stones stolen of those carried to the nest, and the theft success, estimated by dividing the number of stones stolen by the number of theft attempts (successful and unsuccessful). We also calculated and compared the average distance from which stones were carried, and the average size score for both stolen and collected stones for samples from large subcolonies.

The results of interactions between the individual birds stealing stones and the owners of the nests were recorded. We distinguished four types of interactions: (1) theft attempts in which the nest owner did not attack the thief, (2) where the nest owner threatened the thief and the latter retreated, (3) where the thief was pecked by the owner without being injured (mainly in the loin, back or face), and finally (4) when the thief was violently attacked by the mate of the incubating bird.

The effect of availability of stones on the behaviour of relieved birds carrying stones to their nests was studied experimentally in large subcolonies. The control for the experimental group was the sample of individual birds from the same large subcolonies described above. Fifteen stones were added in the vicinity of the nest of the focal individual bird. Stones were placed in between the three or four nearest nests (not nearer to the experimental nest than to any surrounding nest). The distance between the artificially provided stones and the centre of the focal individual's nest was 50–100 cm. The experimentally added stones were obtained from abandoned nests. The selection of the focal individual and the recording of its behaviour were performed following the procedures given above.

To estimate the theft pressure suffered by each occupied nest (i.e. incubating bird) in the subcolonies, we measured the number of stones stolen and the unsuccessful theft attempts in a sample of nests during 30-min periods. In the small subcolonies, this sample was the total number of occupied nests, while in the large subcolonies we selected 50 central nests included in a square marked by 4 wooden sticks. The theft pressure was expressed as the number of stones stolen or unsuccessful attempts per ten nests during 30 mins.

We quantified nest defence behaviour according to Moreno et al. (1995). The nests selected for nest defence tests were spaced out by 3 (in small subcolonies) or 5 nests (in large subcolonies) along transects initiated at the periphery and running along the longest axis of the subcolony. We included only central nests, which we defined as those that were separated by at least two nests from the periphery of the subcolonies. Only penguins incubating two eggs were considered. None of the incubating birds abandoned the nest at the observer's presence. Observations were made on 2 consecutive days to avoid temporal changes in defence behaviour.

Statistical tests employed were one-way and two-way ANOVAs, and ANOVAs for repeated measures. Original data were square root or arcsin transformed prior to statistical analyses to attain normality and homocedasticity. The figures of means and SEs in the tables and text show statistics of untransformed values. All tests performed were two-tailed.

Results

Nest characteristics and stone availability

Nests in small subcolonies had significantly more stones than those in large subcolonies (Table 1). Average stone weight in nest scoops (Table 1) was not significantly different in large and small subcolonies. The number of stones available within subcolonies, between adjacent nests (Table 1), was significantly greater for small than for large subcolonies. The number of stones available on the ground outside the subcolony (up to 5 m from periphery; Table 1) was significantly higher in small than in large subcolonies.

Stone-carrying behaviour

The behaviour of individual birds carrying stones to their nests was different in several aspects in small and large subcolonies (Table 2). Theft intensity (expressed as number of failed attempts, number of stones stolen and percentage of total number of carried stones that were stolen) was significantly higher in large than in small subcolonies. Conversely, the theft success per attempt made was significantly greater for birds from small subcolonies. The proportion of stones carried that were pilfered from temporarily unoccupied nests owned by reproductively unsuccessful pairs did not differ between the two types of subcolonies. The number of stones collected from the ground was also significantly greater in small subcolonies. Nevertheless, the number of stones carried to the nest did not differ significantly between small and large subcolonies. The average size of stones obtained by birds in large subcolonies was significantly greater than that in small ones, although the distance from which stones were obtained did not differ between small and large subcolonies.

In large subcolonies where theft intensity was high, stolen stones were significantly larger than those collected on the ground (stolen: $\bar{x} = 1.85$, SE = 0.161; collected: $\bar{x} = 1.41$, SE = 0.116; $n = 15$ subcolonies in both stolen and collected; ANOVA for repeated measures: $F_{1,14} = 10.18$, $P = 0.006$).

In the majority of the observations of theft attempts ($n = 303$), the thief was threatened by the nest owner (82.8%). In only 9.6% of the theft attempts did the nest owner violently attack the thief (pecks and flipper blows).

Table 1 Number of stones per nest, average weight of stones in the nest scoop, and number of stones available (no./1000 cm^2) in small and large subcolonies (only for stones larger than 1 cm in diameter) ($\bar{x}$ mean, SE standard error) (*F* and *P* refer to one-way ANOVAs)

	Small subcolonies[a]		Large subcolonies[a]			
	$\bar{x}$	SE	$\bar{x}$	SE	*F*	*P*
No. stones per nest	272.2	22.8	166.0	15.0	16.26	<0.001
Average stone weight (g)	19.9	1.6	17.0	1.1	2.09	0.156
No. stones between nests	0.65	0.28	0.05	0.05	4.90	0.033
No. stones 0–5 m outside subcolony	13.78	8.79	5.90	6.61	18.29	0.002

[a] All large colonies had more than 400 nests, those small less than 50. Sample size for each group is 20

Table 2 Behaviour of individual birds carrying stones to their nests in small and large subcolonies. Stones carried also included the number of stones pilfered from temporarily unoccupied nests owned by reproductively unsuccessful pairs, in addition to the number of stones stolen from nests occupied by an incubating individual, and those collected from the ground (*F* and *P* refer to one-way ANOVAs)

	Small subcolonies[a]		Large subcolonies[a]			
	$\bar{x}$	SE	$\bar{x}$	SE	*F*	*P*
Stones carried[b]	9.0	1.4	7.4	1.4	0.74	0.396
Stones stolen[b]	0.6	0.3	2.8	3.9	19.62	<0.001
Unsuccessful theft attempts[b]	0.9	0.4	6.1	1.4	17.21	<0.001
% stones stolen	5.3	2.5	49.3	8.1	43.72	<0.001
% stones stolen from unoccupied nests	3.0	2.3	16.0	7.3	1.94	0.175
Theft success (%)	77.3	9.0	40.7	6.1	7.94	0.009
Stones collected[b]	8.3	1.3	2.5	0.8	17.42	<0.001
Stone size score[c]	1.3	0.1	1.7	0.1	6.10	0.020
Stone-carrying distance (m)	3.3	0.6	5.9	1.2	3.58	0.069

[a] Sample size for each group is 15 individuals
[b] number/15 min
[c] Size was scored as 1 small, 2 medium, 3 large stones (see Methods)

Table 3 Stone-carrying behaviour of individual birds in large subcolonies when stone availability was experimentally increased (15 additional stones). Degrees of freedom were 1,28 in all tests (*F* and *P* refer to one-way ANOVAs)

	Experimental large		Experimental large vs.			
			Large		Small	
	$\bar{x}$	SE	*F*	*P*	*F*	*P*
Stones stolen[a]	0.8	0.4	13.80	0.002	0.12	0.736
Unsuccessful theft attempts[a]	1.8	0.6	8.99	0.012	1.45	0.239
Stones carried[a]	17.9	2.8	14.14	0.002	9.09	0.005

[a] number/15 min. Sample size is 15 individuals

Table 4 Unsuccessful theft attempts, stones stolen and defence rate in small and large subcolonies (*F* and *P* refer to one-way ANOVAs)

	Small subcolonies			Large subcolonies				
	$\bar{x}$	SE	*n*	$\bar{x}$	SE	*n*	*F*	*P*
Unsuccessful theft attempts[a]	0.58	0.28	15	1.00	0.11	15	23.48	<0.001
Stones stolen[a]	0.16	0.10	15	0.61	0.16	15	14.16	<0.001
Defence intensity[b]	19.4	1.95	50	27.0	1.98	50	6.80	0.010

[a] No./10 nests/30 min
[b] No. pecks/30 s

Effects of experimental addition of stones

The mean number of experimentally added stones that were collected by focal individuals was 11.2 in the 15-min sampling period (SE = 1.41, $n = 15$; 75% of experimentally added stones). When stone availability was increased in large colonies, the different measurements of theft intensity decreased (Table 3). None of the behavioural variables quantified differed significantly when comparing the experimental group with small subcolonies (Table 3). However, the total number of stones carried to the nest was significantly higher in the experimental group than in both the large and small control subcolonies (Table 3).

Robbing pressure and nest defence

Both unsuccessful and successful theft attempts per nest were significantly less frequent in small subcolonies than in large ones (Table 4). Nest defence intensity was significantly lower for incubating birds from small than from large subcolonies (Table 4).

Discussion

Several authors have pointed to competition for resources involved in reproduction (nests, nest materials, mates, etc.) as a potential disadvantage of colonial breeding (Alexander 1974; Burger 1981; Wittenberger and Hunt 1985). Competition for nest materials, including theft, has been frequently described, and some potential advantages in stealing them from neighbouring nests instead of collecting them from the surroundings of colonies have been proposed. These advantages include an increased rate of acquisition (Cullen 1957; Burger 1974; Schleicher et al. 1993), a reduced need to leave the immediate area of the nest (Wittenberger and Hunt 1985) or collect in unfamiliar areas (Cullen 1957), energy conservation due to shorter transport distances (Collias and Collias 1978; Wittenberger and Hunt 1985) and the acquisition of materials of better quality (Burger 1974). The descriptions of stealing behaviour suggest that it may also involve costs. Thus thieves have to check if owners are present (Hoogland and Sherman 1976), get involved in fights with nest owners (Balda and Bateman 1972) or run the gauntlet through crowded colonies (Penney 1968). Chinstrap penguins stealing from neighbouring nests obtain larger stones than if they were collecting them between nests or outside the subcolony. This may indicate that the depletion of large stones close to large subcolonies constrains penguins to obtain them through stealing. The fact that thieves are exposed to threats or aggressive attacks by nest owners indicates that the advantages of stealing stones instead of collecting them from the ground must be important for certain individuals to compensate for these disadvantages. Although our results showed that thieves were exposed only very rarely to direct physical attack, the risk of injury, and the possible deletereous consequences on breeding success, may be sufficiently high to select for prudent behaviour.

The prevalence of stealing both in occupied and temporarily unoccupied nests (Moreno et al. 1995) suggests that the availability of stones close to the subcolonies and not already incorporated into nests may be limited. The experiment in which we artificially increased stone availability close to some nests clearly shows that stealing is the consequence of reduced availability of stones close to occupied nests. This effect of reduced availability of nest materials on theft intensity has not been shown before. Subcolony size has a direct bearing on the availability of nest materials. Larger subcolonies imply an increase in availability of materials close to an average nest but also a larger number of potential thieves in the immediate surroundings. Wittenberger and Hunt (1985) suggested that, for an average pair, the two factors could cancel each other, meaning that colony size might not affect the cost-benefit balance involved in theft of nest materials. However, subcolony size may affect the availability of materials not incorporated in other nests. This effect has not been previously reported, but could affect the trade-off between the costs and benefits of stealing in small and large subcolonies.

A larger number of breeding pairs in a subcolony, given a constant nest density, means a reduced surface per nest outside the subcolony from which to obtain stones (Tenaza 1987). This may imply a greater collecting pressure per unit area on the outskirts of large subcolonies compared with small subcolonies, assuming that the distances that penguins are willing to cover in order to collect stones are independent of subcolony size. We have shown that the distance covered by Chinstrap penguins collecting stones is similar in large and small subcolonies. Also, stone availability is lower in the immediate surroundings of large subcolonies. The reduction in availability of stones also applies within large subcolonies. Given this reduced availability of collectable stones and the fact that the risk of flooding by melt water is negatively related to nest size (Moreno et al. 1995), we should expect a higher theft intensity by individuals in large subcolonies and a higher proportion of acquired stones obtained by stealing. The greater tendency to steal stones and the greater dependency on theft for stone acquisition in large subcolonies are very clear in the present study. The higher theft exposure of nests in large subcolonies has in turn led to a more aggressive defence behaviour by nest owners. The higher defence intensity reduces the success of thieves in large subcolonies. In spite of this fact, the best option for acquiring new stones of good size in large subcolonies is to steal from neighbours.

Once stealing stones is performed by several individuals, this behaviour should invade the subcolony. Individuals unable to incorporate new stones through stealing would either expend too much time collecting stones outside subcolonies or see their nests dwindle under the stealing pressure of neighbours. In this social context, the theft effort expended equals the theft pressure suffered for an average individual. Therefore, although the number of stones carried to the nest does not differ between occupants of large and small subcolonies, the number of stones collected anew outside the subcolony for an average nest markedly decreases with increasing subcolony size. Unavoidably, the geometric effects of subcolony size on stone availability lead to a smaller number of stones in nests in large subcolonies, as observed in our study. Thus, subcolonial breeding has negative consequences for nest quality, and consequently for the nest size-dependent risk of flooding (Moreno et al. 1995) in Chinstrap penguins.

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References

Ainley D (1975) Displays of Adélie penguins: a reinterpretation. In: Stonehouse B (ed) Biology of penguins. University Park Press, Baltimore, pp 503–534

Alexander RD (1974) The evolution of social behavior. Annu. Rev. Ecol. Syst. 5:325–383

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

Burger J (1974) Breeding adaptations of Franklin's gull (*Larus pipixcan*) to a marsh habitat. Anim Behav 22:521–567

Burger J (1981) A model for the evolution of mixed-species colonies of Ciconiiformes. Rev Biol 56:143–167

Collias EC, Collias NE (1978) Nest building and nesting behaviour of the sociable weaver *Philetarius socius*. Ibis 120:1–15

Coombs CJF (1960) Observations on the rook *Corvus frugilegus* in southwest Cornwall. Ibis 102:394–419

Cullen E (1957) Adaptations in the kittiwake to cliff-nesting. Ibis 99:275–302

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

Moreno J, Bustamante J, Viñuela J (1995) Nest maintenance and stone theft in the Chinstrap penguin *Pygoscelis antarctica*. I. Sex roles and effects on fitness. Polar Biol 15:533–540

Penney RL (1968) Territorial and social behavior in the Adélie penguin. Antarct Res Ser 12:83–131

Pomeroy DE (1978) The biology of Marabou storks in Uganda. 2. Breeding biology and general review. Ardea 66:1–23

Sapin-Jaloustre J, Bourlière F (1951) Incubation et développement du poussin chez le Manchot Adélie *Pygoscelis adeliae*. Alauda Rev Int Ornithol 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

Sladen WJL (1958) The pygoscelid penguins, Parts 1 and 2. Sci Rep Falkland Islands Dependency Surv 17:1–97

Spurr EB (1975) Communication in the Adélie penguin. In: Stonehouse B (ed) Biology of penguins. University Park Press, Baltimore, pp 449–501

Tenaza R (1971) Behavior and nesting success relative to nest location in Adélie penguins (*Pygoscelis adeliae*). Condor 73:81–92

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 (1975) Microclimate, climate and breeding success in Antarctic penguins. In: Stonehouse B (ed) Biology of penguins. University Park Press, Baltimore. pp 397–409