INFLUENCE OF NEST LOCATION, DENSITY AND TOPOGRAPHY ON BREEDING SUCCESS IN THE BLACK-BROWED ALBATROSS *THALASSARCHE MELANOPHRIS*

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SUMMARY

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The Black-browed Albatross *Thalassarche melanophris* is a long-lived procellariiform that typically nests colonially and exhibits low fecundity. Previous studies on albatrosses have focussed on the bottom-up effects of food supply and their impact on breeding success and have ignored the potential deleterious consequences of top-down predation. To determine whether nest position and adult age influence breeding success, and whether there is evidence that predation affects reproductive output, we investigated relationships between characteristics and location of nesting sites within a breeding colony, age structure, and short- and long-term reproductive output of breeders. Our results are consistent with studies conducted on other colonially breeding seabirds, in that peripheral breeders perform considerably less well than do core breeders, but differ in that nest position was not found to be related to adult age. The timing of failure was affected by nest position, with peripheral nests significantly more likely than core nests to fail during chick rearing. The results suggest that predation is the cause, acting in a non-uniform fashion, because Brown Skuas *Catharacta* [*antarctica*] *lonnbergi* and Giant Petrels *Macronectes* spp. both appear to target more accessible nests on the periphery of colonies. This behaviour could potentially expose a greater proportion of birds to predation if colony sizes diminish in tandem with the decline in albatross populations currently being observed worldwide.

Key words: Seabirds, Black-browed Albatross, *Thalassarche melanophris,* procellariiform, reproductive success, predation, South Georgia, nest location

INTRODUCTION

For seabirds in general, much consideration has been given to the effects on reproductive performance of nest site selection, adult age and experience, and predation. Nest location and adult experience have been linked with breeding success, and nest location has been found to influence predation rates directly (Furness 1984, Emms & Verbeek 1989, Suryan *et al.* 2006). Geographic distribution of seabirds on breeding islands can also be influenced by long-term predation pressures (Phillips *et al.* 1998). In addition, several studies have demonstrated marked differences in the age or quality of birds nesting on the periphery of colonies as compared with those nesting in the core, with resultant effects on breeding success (Coulson 1968, Coulson & Thomas 1985, Becker 1995, Andrew & Day 1999). Indeed, it has been demonstrated that the breeding performance of younger birds improves if those birds are given the opportunity to move to more central sites (Potts *et al.* 1980).

Even amongst seabirds, the Procellariiformes (albatrosses and petrels) exhibit some of the most extreme life history traits: very high adult survival rates, low annual reproductive output and long-deferred sexual maturity (Warham 1990, Prince *et al.* 1994, Weimerskirch 1998). Investigations into the causes of low reproductive output amongst these long-lived birds have long

focussed on the bottom-up effects of food supply (Bolton 1995, Weimerskirch *et al.* 1997, Croxall *et al.* 1999, Huin *et al.* 2000). This approach may be based on an assumption of life-history theory, in which, for such long-lived species, the rearing of offspring is not expected to significantly affect future adult survival (Stearns 1992). Much less consideration has been given to the potential effects of top-down predation on breeding success. In particular, few studies have examined the importance of nest location in Procellariiformes, even though location could be a critical determinant of egg and chick survival, particularly in surface-nesting species.

Avian predators that exploit seabird colonies often take significant numbers of eggs, young or adults (Uttley *et al.* 1989, Hatch & Hatch 1990, Phillips *et al.* 1999, Parrish *et al.* 2001); in extreme cases, they can be the primary cause of localised population decline (Parrish *et al.* 2001). On sub-Antarctic islands, there are three principal avian predators: the Brown Skua *Catharacta* [*antarctica*] *lonnbergi* and the Northern *Macronectes halli* and Southern *M. giganteus* Giant Petrels (Hunter 1983, Reinhardt *et al.* 2000, Phillips *et al.* 2004). The Brown Skua and the Northern Giant Petrel have both increased in numbers at Bird Island and other sites over the past 30 years [Phillips *et al.* 2004, Patterson *et al.* 2008, British Antarctic Survey (BAS) unpub. data], and observations by Catry *et. al.* (2006b) of Grey-headed Albatrosses *Thalassarche chrysostoma* nesting in

neighbouring colonies to Black-browed Albatrosses on Bird Island found high incidences of predation by Brown Skuas during early chick-rearing. Increasing predator populations may influence the productivity and population dynamics of their main prey, and this influence would be particularly pertinent for albatrosses and large petrels, whose populations are already threatened by increased incidental mortality in fisheries, which for some species involves a substantial reduction in survival rate from fledging to recruitment (Weimerskirch *et al.* 1997, Croxall *et al.* 1998).

We present the results of a two-year study conducted on the Black-browed Albatross *Thalassarche melanophris* at Bird Island, South Georgia (54°00′S, 38°03′W), investigating relationships between adult age and quality, nest location and failure rates. Nest site fidelity is very high in Black-browed Albatrosses, with 93% of intact pairs using the same nest in consecutive breeding seasons (Tickell & Pinder 1975), suggesting few incentives to move and therefore presumably little advantage to a specific site. To elucidate this hypothesis, we tested

- whether probability or timing of nest failure was related to nest position or topography, and

- whether there were differences in age or quality (consistent long-term breeding output) of adults nesting peripherally or centrally within the colony.

METHODS

Field data collection

Data were collected at a long-term study colony of Black-browed Albatrosses at Bird Island, South Georgia. Ringing and resighting of adults and chicks at this colony has been carried out intermittently since austral summer 1975/76, with intensive breeding and demographic information acquired annually since 1995/96 (Prince *et al.* 1994). Annual counts indicate that the colony has declined in size by 3%–4% per year since the early 1990s (BAS unpub. data). In the two years of this study (2004/05 and 2005/06), the number of active nests was 217 and 198 respectively. The colony was surveyed daily from the arrival of the first adult (approximately mid-October) until the end of brood-guard (approximately mid-February), and on average every three days thereafter. Bird rings and Darvic numbers (large coloured identifying rings), egg-laying and nest failure dates were recorded on each occasion. Over the two-season study, both parents were identified at 384 of the 415 nests (92.5%), and only one parent at the remainder (nests that failed early).

A standard inclinometer was used to measure planar slope (to the nearest degree) for each nest site in the colony. At the time of nest failure or chick fledging, the distance to the nearest neighbour was also measured using a Leica Disto Classic 3 laser (Leica Geosystems, Heerbrugg, Switzerland) measurement tool. The measurement was taken from the centre of the failed nest to the centre of the nearest active neighbouring nest at a height of 1.5 m (which cleared the numerous low-level tussock mounds and rocks). The number of active neighbours within a five-metre radius of the focal nest was also recorded, providing a measure of changes in local breeding density over time in the colony.

After all pairs had laid their eggs, nests were classified as either "peripheral" (on the outermost boundary of the colony) or "core" for the duration of that season. For all core nests, the minimum

distance from nest centre to the colony boundary (assuming that this measurement corresponded to a straight line joining the distal margin of adjacent nests on the colony margin) was measured using the Leica Disto tool.

Data analysis

Based on the detailed monitoring carried out at the colony since 1995/96, a long-term success score (hereafter "breeding score") was calculated for each individual as the mean number of chicks fledged per year from the first season in which the bird was recorded breeding (i.e. laying and failing was deemed equivalent to deferring breeding). For each nest for which both parents were identified, the mean breeding score was used in subsequent analyses (conclusions were the same if analyses were performed using one parent chosen at random). Where the identity of only one parent was known, the score for that individual was included. In total, 190 of the 469 birds in this study (40.5%) were of known age. For each nest, the age of the only adult of known age, or the mean age of both adults (if known), was used in further analyses (conclusions were the same if using one randomly selected age).

The influence of nest characteristics (slope, distance to nearest neighbour, number of active nests within a five-metre radius, and distance to colony edge) on the likelihood of successful breeding (success or failure to fledge a chick) was examined using binary logistic regression. To assess whether adult age or breeding success influenced nest outcome, we initially used the Mann–Whitney U- and G-tests to compare breeding success and timing of failure between peripheral and core nests; we then used binary logistic regression analysis to identify whether adult age or quality (reflected by long-term breeding score) was the dominant factor.

For pairs that bred together in both years of the study, data were included in analyses from a single season, selected at random, to avoid pseudo-replication. This approach resulted in 245 breeding attempts available for analysis from the total of 415 recorded over the two seasons. All analyses were undertaken using Microsoft Excel 2000 (Microsoft Corporation, Redmond, WA, USA) and Minitab for Windows (version 14: Minitab, State College, PA, USA).
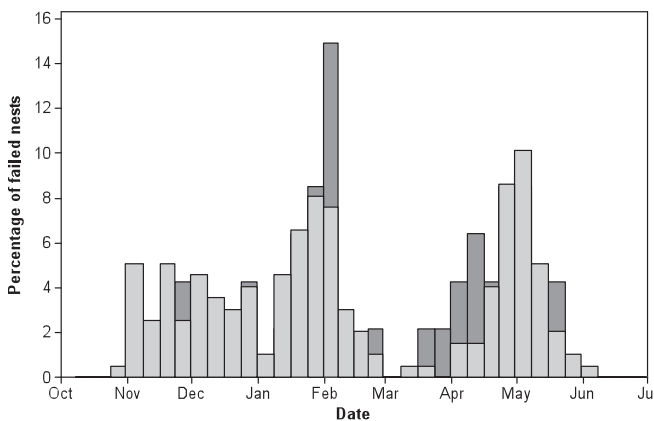
RESULTS

Fig. 1 indicates the distribution of dates of failure throughout the whole breeding season. Overall, nest failure rates peaked in early February, with a secondary peak at the start of May. From a temporal perspective, the proportion of nests that failed during incubation was similar in core and peripheral nests, and although peripheral nests appeared more likely to fail during chick-rearing (Table 1). The difference was marginally nonsignificant (*G*-test: $G = 5.55$, $P = 0.062$).

Testing the influence of nest-site characteristics, we found significant relationships for the number of nests within five metres ($P = 0.004$) and for distance from the colony edge ($P = 0.019$) with the probability of successful breeding (binary logistic regression: $G_4 = 16.001$, $P = 0.003$; Hosmer–Lemeshow (2000) goodness of fit: $\chi_8 = 3.197$, $P = 0.921$). The characteristics of slope and distance to nearest neighbour did not show significant effects. Therefore, compared with nests that failed, nests from which chicks fledged tended both to be further from the colony edge and to have a higher number of neighbours. However, the relationship between success

and number of neighbours was confounded by the seasonal decline in density, because the number of occupied nests within a five-metre radius was recorded on the date of fledging or failure, and this number was declining over time regardless of outcome (Pearson correlation: $r_{243} = -0.571$, $P < 0.001$; Fig. 2). This observation is unsurprising, because as more nests fail, fewer are left in the colony. Nonetheless, at the time of fledging, successful nests had considerably more near neighbours than did those that failed during the same period (Fig. 2).

We observed a highly significant correlation (Pearson correlation: $r_{50} = 0.466$, $P = 0.001$) for the age of parents at study nests and a positive correlation (Spearman rank correlation: $r_s = 0.284$, $P = 0.03$) for mean adult age at nests with mean breeding score. With these variables both available for entry into the model (binary logistic regression: $G_2 = 7.649$, $P = 0.022$; Hosmer–Lemeshow (2000) goodness of fit: $\chi_8 = 7.684$, $P = 0.465$), birds nesting in the core had significantly higher mean long-term reproductive scores as compared with birds nesting at the colony edge ($P = 0.019$), but no significant age differences between edge and core were observed ($P = 0.821$). Increasing the sample size by inclusion of birds of unknown age showed the same pattern, with a greater median long-term reproductive score for pairs (n = 198) at core nests as compared with pairs (n = 47) nesting on the periphery (Mann–Whitney U-test: $U = 1311.0$, $P = 0.008$).

Fig. 1. Timing of nest failure throughout the breeding season in Black-browed Albatrosses *Thalassarche melanophris*. The darker portion of each bar indicates results from peripheral nests; the lighter portion, results from core nests. Data are grouped by week.

TABLE 1
Breeding outcomes at core and peripheral nests in Black-browed Albatrosses *Thalassarche melanophris*

	Failures		Fledged successfully [n (%)]	Nests (n)
	Pre-hatching (egg stage) [n (%)]	Post-hatching (chick stage) [n (%)]		
Colony periphery	14 (30)	28 (60)	5 (10)	47
Colony core	68 (34)	85 (43)	45 (23)	198

DISCUSSION

Our results indicated that Black-browed Albatrosses nesting further from the edge of the colony were consistently more productive in the long term. This finding accords with studies conducted on other seabirds (Tenaza 1971, Siegel-Causey & Hunt 1981, Stenhouse *et al.* 2000). No relationships with likelihood of successful breeding were apparent for distance to nearest neighbour or nest slope, but chicks that fledged successfully did so from nests with more near neighbours (Fig. 2). Therefore, although nesting centrally may enhance reproductive success, the density of surrounding nests is also an important determinant of chick survival. Other studies have found positive, curvilinear or negative relationships between breeding success and density (Davis & Dunn 1976, Parsons 1976, Furness 1984). In a review of the subject, Wittenberger & Hunt (1985) suggested that predator type is the main determinant of the relationship between density and success, with higher numbers of neighbours at close proximity able to mount a stronger collective anti-predator response. Their hypothesis was confirmed in subsequent studies in which avian predators were the main threat to nest survival (Becker 1995, Phillips *et al.* 1998).

Our results showed no evidence of any age differences between adults on the edge of the colony and those located in the centre. This finding is inconsistent with those of many other studies conducted on seabirds, in which proportionally more birds of younger age are found on the periphery (Coulson 1968, Porter 1990, Andrew & Day 1999). The explanation may be that, because of the ongoing and rapid population decline in Black-browed Albatrosses at South Georgia, there are usually newly vacant sites available in the centre of colonies where recruits can readily become established. Failures from young breeders in central locations would further aid colony fragmentation.

Previous research has shown that young birds usually initially experience poor breeding success (Parsons 1976, Coulson & Thomas 1985, Klomp & Furness 1991), but as age-related experience accumulates, reproductive output increases (Weimerskirch 1992, Dittmann & Becker 2003, Ludwigs & Becker 2005). This pattern was clearly demonstrated in our study. Whilst more detailed cross-sectional and longitudinal analysis would be necessary to identify the underlying causes of these relationships, our results suggest that nest position is not a contributing factor and that alternative
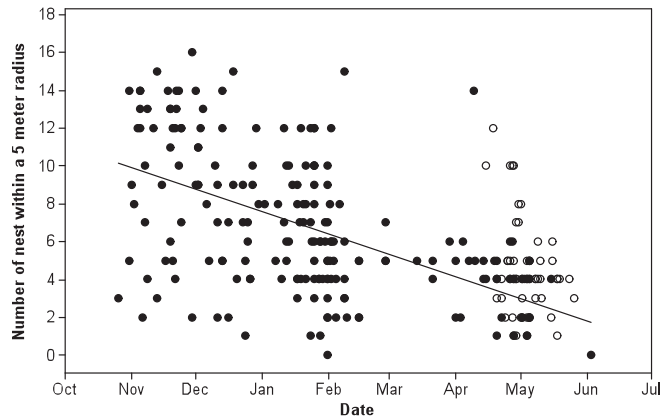
Fig. 2. Comparison between successful nests (open circles, n = 50) and failed nests (filled circles, n = 195) by the number of neighbours within a 5-m radius. Line shows least squares regression for failed nests only.

explanations, such as the progressive appearance or disappearance of phenotypes, age-related improvements in competence, or optimisation of breeding effort are more likely to be responsible (Forslund & Pärt 1995).

Consistent with many other studies, one of our clearest findings was the distinct disadvantage of nesting on the colony edge as compared with the core in terms of likelihood of successful breeding (Patterson 1965, Aebischer & Coulson 1990, Andrew & Day 1999, Stenhouse *et al.* 2000). Whether this disadvantage reflects differences in parental quality rather than nest location *per se* is difficult to determine. However, the timing of nest failure may provide a clue: edge nests were more likely than core nests to fail during chick-rearing; little difference in success during incubation was observed (Table 1).

At Bird Island, incubation failures in Black-browed Albatrosses result almost exclusively from abandonment of the nest when a bird's partner fails to return in time from the sea, which is likely to reflect to some extent intrinsic characteristics such as adult age and quality (Catry *et al.* 2006a, 2006b). This observation is corroborated by the fairly uniform distribution in timing of nest failure within the early breeding season (Fig. 1). By comparison, failures during chick-rearing are clustered in two periods: The first occurs between mid-January and early February, accounting for around 30% of all egg and chick mortality combined. The second occurs during late April/early May, accounting for approximately 20%. The first period corresponds with the end of brood-guard, when chicks are first left alone to fend for themselves. This is the time when most predation by skuas is observed, both in this species and in the Grey-headed Albatross, which breeds in neighbouring colonies (Catry *et al.* 2006b, BAS unpub. obs.). The second peak, in April/May, corresponds with a high level of observed predation by the two species of giant petrel (BAS unpub. obs.). Identifying the predators responsible for failures at a specific site is extremely difficult: it would require an almost 24-hour human presence in the colony (indeed, most nests fail overnight) or a sophisticated visual recording method. However, indirect evidence and opportunistic observations suggest strongly that predation pressure is greatest on accessible nests on the periphery of the colony, which may to a large extent be independent of intrinsic quality of the parents and of chick condition.

CONCLUSIONS

Our study has demonstrated, for the first time in an albatross, a clear association between nest location and breeding success that is independent of adult age. The demographic impact is likely to increase over the long term as mean colony sizes diminish in tandem with declining albatross populations. The subsequent changes in colony geometry could also result in a proportional increase in the vulnerability of birds to predation, as proposed for fragmenting penguin colonies (Jackson *et al.* 2005). Given the increase in populations of both skuas and giant petrels, which are important predators at most sub-Antarctic islands, such effects could prove to be of considerable importance for many surface-nesting species.

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