ORIGINAL PAPER

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Chick survival in relation to nest site: is the Antarctic petrel hiding from its predator?

Abstract In birds, the characteristics of the nest site may affect reproductive success. We found that shelter is an important characteristic of the Antarctic petrel (*Thalassoica antarctica*) nests because shelter prevents chick predation. However, the benefit of shelter was countervailed by melt water which mainly entered well-sheltered nests. Chick survival was monitored until the chick was left unattended for the first time. Late-hatched chicks had a higher survival probability than early-hatched chicks, possibly because late hatchers swamp the predator, the south polar skua (*Catharacta maccormicki*). Poorly sheltered nests tended to be occupied by parents with low body mass and late-hatched eggs. The results suggest that both shelter per se and parental characteristics may explain the relationship between predation risk and shelter. We need experiments to study the influence of nest site on reproductive success, and we need to map the frequency of melt water as a cause of reproductive failure.

Introduction

For colonial birds, the effects of breeding habitat have been investigated on several spatial scales, and differences in reproductive success have been found between sub-colonies (e.g. Barbosa et al. 1997), between central

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and peripheral parts (e.g. Coulson 1968), and between particular areas or patches of the colony (e.g. Danchin et al. 1998; Regehr et al. 1998). On these spatial scales, individuals may select breeding habitat by assessing the quality of patches based on the reproductive success of conspecifics (Boulinier and Danchin 1997; Danchin et al. 1998). However, nests within patches may also be of different suitability for breeding (e.g. Regehr et al. 1998; Velando and Freire 2003; Weidinger 1998). Therefore, the optimal breeding habitat may not be achieved only by comparing the success of conspecifics between patches, but also by evaluating the physical characteristics of nest sites within patches (Kokko et al. 2004). Hence, there is a need for studies describing the variation in nest site quality within patches, and relating nest site characteristics to reproductive success.

The potential advantage for individuals occupying nest sites with certain characteristics can be studied by comparing the characteristics of successful and unsuccessful nests (e.g. Clark and Shutler 1999). However, parents of high quality may occupy the best nest sites, which makes it difficult to deduce any causal relationship between nest site characteristics and reproductive success (cf. Coulson 1968). Nevertheless, if there is a relationship between parental quality and nest site characteristics, this may indicate the quality of the nests because competition should result in high quality individuals at the most suitable nest sites (e.g. Porter 1990; Potts et al. 1980).

Predation is an important factor causing egg and chick loss in birds (Ricklefs 1969), but shelter around the nest may reduce predation risk. Species in the order Procellariiformes are either burrow nesting and well protected from avian predators, or surface nesting such as the Antarctic petrel *Thalassoica antarctica*, with nests exposed to avian predators (Warham 1990). We report from a colony in Antarctica where the south polar skua *Catharacta maccormicki* is responsible for substantial losses of Antarctic petrel eggs and chicks (Haftorn et al. 1991a). The skuas hunt by searching for nests where Antarctic petrel eggs or chicks are unprotected (Haftorn

et al. 1991b). The chicks are often snatched while the skua is in the air, and the skua is rarely observed on ground in the petrel colony, except at a few lookouts (personal observation). This is probably due to the high breeding density of Antarctic petrels and their ability to spit stomach oil on intruders (Warham 1977; Weidinger 1998; but see Van Franeker 2001). The Antarctic petrels do not shape the nest site to achieve shelter, but some nests are exposed and unprotected, whereas others are located between rocks and even in shallow crevices.

We hypothesised that well-sheltered nests are best suited for Antarctic petrels because these nests are more difficult for the south polar skua to observe. Furthermore, in well sheltered nests it may be easier for the parent to protect the chick and for the chick to defend itself. Consequently, we predicted that successful nests have more shelter than unsuccessful nests and that parental quality is positively related to shelter. As a measure of reproductive success, we used chick survival during the guarding period, and for this period we also investigated whether chick survival was related to hatching date. As potential indicators of parental quality, we used adult body mass and hatching date (see parental characteristics below).

Materials and methods

Study area and study species

The fieldwork was carried out at Svarthamaren (71°53′S, 5°10′E), continental Antarctica, in January–February 2001. About 200,000 pairs of Antarctic petrels breed at Svarthamaren, a colony located about 200 km from the coast (Mehlum et al. 1988). Additionally, about 90 pairs of south polar skuas breed at this site, and during breeding they rely completely on petrel eggs and chicks for food (Brooke et al. 1999). The nests of the Antarctic petrel are densely located ($\sim$0.8 breeding pairs per m^2) on steep rocky slopes (Mehlum et al. 1988), and the nests are often placed close to rocks, but the size and number of rocks vary. Some nest sites have walls and even a roof, whereas others have no shelter. The nest is a shallow depression, usually with small stones and some feathers as the only nest material (Haftorn et al. 1991a). Although far outnumbered by Antarctic petrels, snow petrels *Pagodroma nivea* also breed at Svarthamaren at well protected nest sites that seem unsuitable to the larger Antarctic petrel.

The breeding cycle of the Antarctic petrel is well synchronised. The single egg is laid at the end of November and hatches in mid-January (Lorentsen and Røv 1995). Here, the eggs hatched between 5 and 19 January ($\bar{x}$ = 12.1, SD = 2.0, n = 505). After hatching, the parents subsequently guard the chick to protect it from south polar skuas and harsh weather. The guarding lasts 7–15 days and consists of one to four guarding spells (Lorentsen and Røv 1995; Tveraa et al. 1998a; Varpe et al. 2004). If the parents are unable to

co-ordinate the guarding spells, the chick is left early, and the predation risk of the chick may increase (Tveraa et al. 1998a; Varpe et al. 2004).

Shelter, sample and fates

Prior to hatching, nests were scored for shelter by rocks, leaving 505 nests at hatching. The nests were scored on a scale from 1 to 5: (1) no rocks as shelter, (2) a smaller rock close to the nest, or a larger rock 0.5–1.0 m from the nest, (3) two or more smaller rocks at more than one side, or shelter from one side and a roof, or a single rock more than 0.5 m high and closer than 0.5 m, (4) shelter from three sides or two sides and a roof, and (5) shelter from three sides and a roof. Five days after the first scoring, 50 nests were scored again by Ø.V. and for the first time by T.T. The repeatability was high both within and between measurer (Table 1). Many nests had some shelter (score 2 and 3), but few nests had shelter on most sides (score 4 and 5) (Fig. 1). Only 2% of the nests had score 5, and these nests were combined with the nests with score 4 in the statistical analyses. Some scored nests

Table 1 The repeatability in shelter scores within and between measurer, based on a subsample of 50 Antarctic petrel nests

Original score	Repeated score by the same measurer					Repeated score by another measurer				
	1	2	3	4	5	1	2	3	4	5
1	**6**					**3**	3			
2	2	**24**	1			5	**19**	2	1	
3		4	**10**				5	**9**		
4			1	**1**				2		
5					**1**					1

Shelter is the degree of rocks surrounding the nest, where score 1 is given to nests with least shelter. The number of nests given the same score as the original is marked in bold
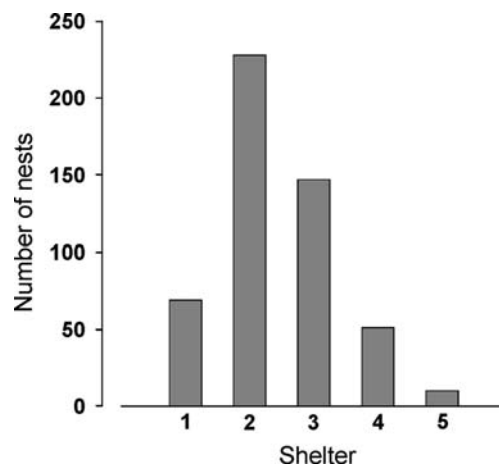

Fig. 1 The distribution of Antarctic petrel nests in relation to shelter at the time of hatching (n = 505). Shelter is the degree of rocks surrounding the nest, where category 1 has least shelter. Nests with score 4 and 5 were combined in the statistical analyses

were part of a chick exchange experiment that started 1–4 days after hatching (Varpe et al. 2004). This limited the number of nests that could be used for the present study. For the analysis of body mass in relation to nest site, we included all nests except those where the parents were weighed after the treatment had started. For the analysis of chick survival during guarding, we included the control nests from the experiment (where chicks of equal age were exchanged between nests shortly after hatching) in addition to the nests monitored only for the present study. Because of this selection, and because we did not manage to weigh the parents at all scored nests, the sample size varied for the different analyses. The sample sizes or degrees of freedom are reported for each analysis.

To monitor chick fate, each nest was visited daily until the chick was observed alone at the nest for the first time, i.e. to the end of the 7–15 days long guarding period. Due to logistical constraints, the study could not continue until fledging. We used three fate categories: (1) predation, when a chick disappeared between two visits to the nest; (2) death, when a chick was found dead in the nest; (3) melt water, when a chick disappeared or was found dead, but where melt water had already entered the nest and weakened the chick. We refer to chick survival when all fates were analysed simultaneously, but when analyses were performed with predation as the only fate, we refer to predation risk. At five nests, the parent on guard flew off the nest because of our presence, and did not return in time to prevent predation. We omitted these nests from further analyses, but all these nests had little shelter (score 1 or 2).

Parental characteristics

In the Antarctic petrel, parental body mass, when standardised within sex, is an indicator of parental quality. Parents that are heavy when they return from a foraging trip, due to high foraging success (Tveraa et al. 1997), do better at the nest. They incubate or guard longer compared to birds with low body mass (Tveraa et al. 1997, 1998a; Varpe et al. 2004). Parents with high body mass also give more food to the chick (Lorentsen 1996; Tveraa et al. 1998b), and their chick have higher growth rates (Lorentsen 1996). Comparisons of parental body mass is best done at the start of a guarding spell, because this ensures that the birds have newly arrived from a foraging trip and therefore have not spent a varying number of days feeding the chick and fasting at the nest. Consequently, we used the body mass of parents weighed upon arrival to the first guarding spell after hatching. Because body mass is positively correlated with structural body size, we used structural body size (see Varpe et al. 2004 for details) as a covariate in analyses of body mass differences between shelter categories. Adults were weighed to the nearest gram.

Effects of hatching date on reproductive success have not been reported for the Antarctic petrel, but early breeding is often associated with high reproductive success, and parental quality often plays a part when this pattern is explained (Nilsson 1999, for a review). We therefore tested if the hatching date differed between shelter categories.

Statistical analyses

Differences in body mass between shelter categories were tested with analyses of covariance and differences in hatching date with analyses of variance. F statistics based on type III sums of squares are reported. Survival data were analysed using logistic regression models with the logit link function and binomial distribution, and the parameter estimate β and a 95% confidence interval (CI) are reported (Allison 1999). The Akaike information criterion (AIC) was used to select the most suitable model for predicting chick survival and predation risk, with shelter, hatching date and the two-way interaction as variables. Adult body mass was not known prior to hatching and could not be included. Model selection was done based on AIC values (e.g. Burnham and Anderson 1992) with the stepAIC function in R (R Development Core Team 2004; Venables and Ripley 1999). The SAS software (SAS Institute Inc. 1990) was used for the other analyses.

Results

During guarding, 16% of the 326 pairs lost their chick; 34 chicks were taken by south polar skuas, six chicks were found dead in the nest, and 12 chicks were lost after melt water had entered the nest. Predation often occurred soon after hatching (58% of the lost chicks
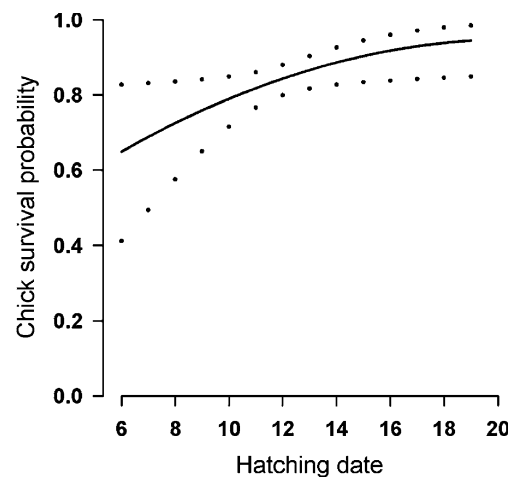
Fig. 2 Chick survival during the guarding period in relation to hatching date (January 2001) in the Antarctic petrel. The predicted survival probability (*line*) with upper and lower confidence intervals (*dotted*) are from a logistic regression, $df = 324$, Pearson $\chi^2 = 332$

Table 2 Model selection for the analyses of chick predation risk and chick survival probability in the Antarctic petrel during the guarding period

Shelter	Hatching date	Shelter × hatching date	k	AIC	Diff AIC
Predation risk[a]					
x	x	x	8	214.4	5.3
x	**x**		**5**	**209.1**	**0.0**
x			4	215.0	5.9
	x		2	211.2	2.1
			1	215.2	6.1
Chick survival[b]					
x	x	x	8	291.5	6.3
x	x		5	286.9	1.7
x			4	291.1	5.9
	x		**2**	**285.2**	**0.0**
			1	288.1	2.9

Variables included in each model are marked with x. The selected model is in bold. The number of parameters in the model (k), the Akaike information criterion (AIC), and the difference in AIC between selected and given model (diff AIC) are reported

[a]Chicks that disappeared between two visits to the nest were regarded as having been preyed upon. For the full model $df = 297$, Pearson $\chi^2 = 303$

[b]Chicks found dead and chicks lost due to melt water were also included. For the full model $df = 318$, Pearson $\chi^2 = 326$

were lost by the third day). Two-thirds of the losses were due to melt water that occurred on 9 and 11 January during a period with overcast weather. Where the chick was taken by south polar skuas, the parent was sometimes still at the nest on our first visit after predation had occurred (28% of the cases), otherwise the nest was empty and the parent had left, possibly before the chick was preyed upon.

Late-hatched chicks had higher survival probability than early-hatched chicks ($\beta = 0.18$, CI: [0.02, 0.34], Fig. 2). Simil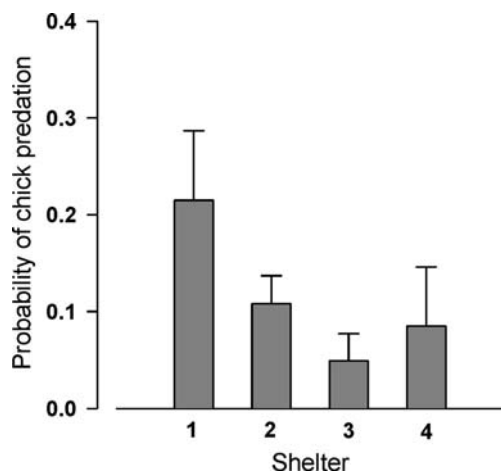arly, for analyses with predation as the only fate, chicks hatching late were less likely to be preyed upon ($\beta = -0.24$, CI: [−0.44, −0.05]. There was no difference in the duration of the guarding period between shelter categories ($F_{3,256} = 0.7$, $P = 0.54$); hence, the shelter categories can be compared directly with respect to survival probability. However, parents guarded the chick longer if hatching was early (linear regression: $r = -0.21$, $n = 260$, $P < 0.001$).

In the order of explained deviance, hatching date and shelter are suggested to predict predation risk whereas only hatching date is suggested to predict chick survival (Table 2). The predation risk was higher in poorly sheltered nests (Fig. 3). In contrast, some chicks in well-sheltered nests were lost due to melt water whereas this risk was absent in poorly sheltered nests (no statistical tests performed due to few losses; 0, 1, 6 and 5% lost in shelter category 1–4, respectively). Consequently, there seem to be two risks; predation mainly affecting poorly
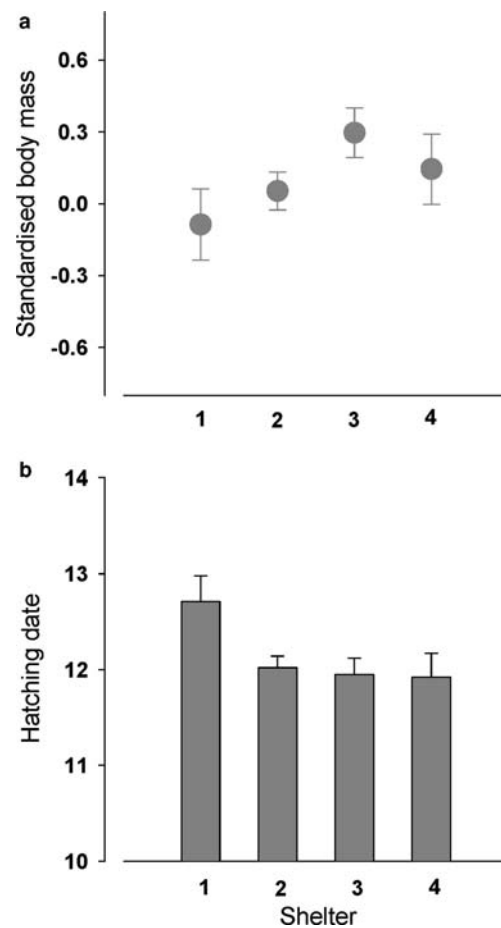
Fig. 3 Predation risk during the guarding period in relation to shelter in the Antarctic petrel. Shelter is the degree of rocks surrounding the nest, where category 1 has least shelter. Hatching date is controlled for, and the bars are least-square means with SE from a logistic regression

Fig. 4 Parental body mass and hatching date (means with SE) in relation to shelter in the Antarctic petrel. Shelter is the degree of rocks surrounding the nest, and category 1 has least shelter. **a** Adult body mass as least square means after body size was included as a covariate, measured at the start of the first guarding spell after hatching, with sample size 35, 122, 71 and 35 for shelter category 1–4, respectively. Body mass was standardised to a mean of zero and variance of 1 within each sex to facilitate direct comparison between individuals of different sex. **b** Hatching date (January 2001) with sample size 69, 228, 147 and 61

sheltered nests and the countervailing risk of melt water mainly affecting well-sheltered nests. Therefore, shelter was important in explaining the deviance in predation risk but not in chick survival. The importance of shelter was detected due to the detailed monitoring of chick fates.

Parents that occupied well-sheltered nests were heavier than those in poorly sheltered nests ($F_{3,259} = 3.1$, $P = 0.03$), but when body size was controlled the difference was not statistically significant ($F_{4,258} = 1.8, P = 0.14$, Fig. 4a). There was no consistent relationship between body size and shelter (males: $F_{3,401} = 0.4$, $P = 0.78$, females: $F_{3,371} = 2.0$, $P = 0.12$). Hatching occurred later in the least sheltered nests ($F_{3,501} = 2.7$, $P = 0.04$, Fig. 4b). Hatching date was not correlated with adult body mass, male body size or female body size (linear regression: $r = -0.04$, $n = 262, P = 0.48$; $r = -0.06, n = 405$, $P = 0.25$ and $r = -0.05$, $n = 375, P = 0.33$, respectively).

Discussion

Chick survival and hatching date

Chick survival during guarding was intermediate compared to earlier seasons (Sæther et al. 1997; Tveraa et al. 1998a), and predation was the most important mortality factor, as observed earlier in the same colony (Haftorn et al. 1991a). Previously, it has not been recorded whether nests were exposed to melt water, although many eggs and chicks were lost during a heavy snowfall at the time of hatching in 1993 (Sæther et al. 1997). However, the melt water observed in the present study emerged from the partly frozen, snow-free ground.

The highest chick survival (and lowest predation risk) was associated with late hatching (Fig. 2). This is contrary to the pattern observed in many other seabirds (Brouwer et al. 1995; Ollason and Dunnet 1978; Spear and Nur 1994; Weidinger 1998), but lower breeding success has also been observed for pairs laying early (Hatch 1990). For instance, Rodway and Regehr (1999) observed an unusually late arrival of the main food source, which resulted in an advantage for late-hatched herring gull *Larus argentatus* chicks. Foraging conditions improving with time may also explain the higher survival of late hatchers in the present study. However, the data suggest little variation in foraging conditions at the time of guarding because the parents' arrival mass to the first guarding spell was not related to arrival date (linear regression: $r = -0.04, n = 263, P = 0.50$).

Alternatively, the positive relationship between chick survival and hatching date may be a result of predator-swamping (Ims 1990). Brooke et al. (1999) found that food was scarce for the south polar skuas in the colony during late incubation, probably limiting the number of skuas breeding there. However, when the majority of Antarctic petrel chicks are left unattended, food may be ample to the south polar skuas (Haftorn et al. 1991b). Hence, early-hatched chicks may experience higher predation risk during guarding than late-hatched chicks. Although late hatching may increase the survival probability through the guarding period, this strategy may not be adaptive because fledging success or post-fledging survival may be low for late breeders, particularly during the short breeding season at high latitudes (Moreno et al. 1997). Consequently, Antarctic petrels may benefit from synchronous hatching to avoid predation shortly after hatching, and to breed early enough to avoid low fledging success. We observed that parents guarded the chick longer if hatching was early, which may be a flexible response to achieve synchrony at the end of guarding and thereby reduce predation risk of the chick.

Chick survival and shelter

When all fates were included, there was no support for the predicted relationship between chick survival and shelter, probably because of the unexpected chick mortality caused by melt water in well-sheltered nests (cf. Stokes and Boersma 1998). The melt water had a greater risk of accumulating in nests surrounded by rocks, and melt water often emerged along the sides of rocks, particularly if the rocks were large. It remains to be studied whether melt water entering well-sheltered nests is an unusual event having little effect on the evolution of nest site selection in Antarctic petrels, or whether melt water may counteract the benefits of shelter. The possibility that melting patterns may be sensitive to changes in climate should be kept in mind in future studies of habitat use in the Antarctic petrel (cf. Van Franeker et al. 2001).

The predicted differences in shelter between successful and unsuccessful nests were found when chick predation was studied separately. Chicks in poorly sheltered nests were preyed upon more often compared to chicks in well-sheltered nests (Fig. 3). The vulnerability of unprotected nests is emphasised by the observation that all five chicks lost due to our disturbance (not included in the analyses above) were in nests with little shelter. To our knowledge, only two studies have related reproductive success to nest site shelter in surface-nesting Procellariiformes such as the Antarctic petrel. Weidinger (1998) found that Cape petrel chicks were preyed upon less often by skuas *Catharacta sp.* if the nest had some cover by nearby rocks, whereas no relationship between breeding success and physical protection was found for the fulmar *Fulmarus glacialis* (Falk and Møller 1997). In both these studies, predation was the main mortality factor. Our findings are also comparable to studies on the razorbills *Alca torda* where nests on ledges were more prone to predation than the nests in burrows (Hudson 1982), and where this nest site difference was absent when studied in a colony with little avian predation (Rowe and Jones 2000). The effects of shelter have also been tested experimentally. In a Magellanic penguin *Spheniscus magellanicus* colony, eggs placed at various unoccupied nest sites were at greater risk of

avian predation when the site had little cover (Stokes and Boersma 1998). Furthermore, if the cover was artificially altered, chick survival changed as expected (Stokes and Boersma 1998). Such experiments are important to disentangle the effect of parental quality versus nest site characteristics on reproductive success.

Shelter in relation to parental body mass and hatching date

Our data indicate that heavy parents avoid poorly sheltered nests, but some of the difference in body mass between shelter categories was removed when body size was included as a covariate (Fig. 4A). We are not aware of other studies that have related body mass to nest site characteristics when studying nests within a patch in colonial birds, but differences in body mass have been found between areas in a colony (e.g. Coulson 1968). In our study, there is only limited support for nest site selection resulting from heavy parents occupying well-sheltered nests, despite the importance of body mass in determining many aspects of reproductive success in Antarctic petrels (see parental characteristics above). However, body mass prior to the breeding season may be a better measure of parental quality on the time scale of the whole breeding season, compared to the body mass at the start of guarding as used here.

For other species it is found that age and not necessarily individual quality resulted in selection of nest sites of differing quality often due to earlier arrival of old and experienced birds (e.g. Potts et al. 1980). The age of the birds in the present study was unknown, and the breeding season prior to egg-laying is not yet studied at Svarthamaren.

Although being a measure of parental quality in many species, laying or hatching date is not known to reflect parental quality in the Antarctic petrel. However, hatching was later in poorly sheltered nests (Fig. 4b), but this need not be attributed to parental quality. Instead, birds at these nests may be more disturbed while incubating and therefore have eggs hatching later. Alternatively, later hatching at nest sites with no shelter may be due to later egg-laying, typical of young and inexperienced birds (e.g. Ollason and Dunnet 1978; Potts et al. 1980).

Based on parental characteristics, this study only weakly suggests that some nest sites are of better quality than others, namely those with some shelter around the nest. Studies before egg-laying are needed to understand nest site selection in the Antarctic petrel, preferably in combination with experiments, which disentangle the influence of parental quality and nest site characteristics.

Conclusion

Shelter is a nest site characteristic that seems to prevent chick predation in the Antarctic petrel. It seems important to have at least some shelter around the nest (cf. Stokes and Boersma 1998), but curiously, losses due to melt water may select against using nests with much shelter. However, the tendency to avoid poor shelter, by birds with high body mass and by birds with eggs hatching early, suggests that selection for shelter has been most important in the past. This study and some others (references above) indicate that habitat choice may also influence reproductive success on the smallest spatial scale in a bird colony. We did not study the proximate mechanisms involved in nest site selection, but the use of conspecific reproductive success when prospecting for a breeding patch (Boulinier and Danchin 1997; Danchin et al. 1998) may also be used as a cue within patches in a colony, i.e. on the scale of the single nests (cf. Zicus and Hennes 1989). Alternatively, the choice of breeding habitat may take place in a hierarchical manner where different cues serve as indicators on different spatial scales; the patch may be chosen based on the success of conspecifics (Boulinier and Danchin 1997; Danchin et al. 1998), whereas the nest within the patch may be chosen based on physical characteristics and own experience (Kokko et al. 2004).

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