CAVITY CHARACTERISTICS AND ICE ACCUMULATION AFFECT NEST SELECTION AND BREEDING IN SNOW PETRELS *PAGODROMA NIVEA*

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Received 9 January 2014, accepted 19 August 2014

SUMMARY

EINODER, L.D., EMMERSON, L.M., SOUTHWELL, D.M. & SOUTHWELL, C.J. 2014. Cavity characteristics and ice accumulation affect nest selection and breeding in Snow Petrels *Pagodroma nivea. Marine Ornithology* 42: 175–182.

The choice of particular nesting sites can be important for seabirds breeding in colonies exposed to harsh environments. For polar seabirds of small to medium body size, cavity nesting provides shelter from predators as well as from harsh weather, but cavities may also accumulate snow, which is detrimental to breeding. We studied these relative influences on Snow Petrel *Pagodroma nivea* nest selection at a colony exposed to moderate snowfall and substantial windblown snow from regular katabatic winds. Nest selection was assessed using 13 habitat characteristics compared through three stages of breeding (initial occupancy, incubation and chick provisioning), during two consecutive years of varied weather. Snow Petrels occupied a wide range of cavities, but hatching success and chick survival were greater in more sheltered nests with a flat nest bowl. Ice accumulation was detrimental to laying and breeding success and was related to aspect: nesting cavities on the lee of the island provided some protection against prevailing winds yet were more prone to ice accumulation. The most successful nests had a degree of exposure to winds that allowed them to remain ice-free but enough shelter to retain loose substrate and presumably provide protection from predators.

Keywords: petrel, nest, cavity, preferences, ice, breeding

INTRODUCTION

The selection of a specific site for nesting can have important consequences for reproductive success in birds. Characteristics of the nest and surrounding habitat can provide a range of advantages such as shelter from inclement weather, winds or sunlight (e.g. Lloyd & Martin 2003, Mallory & Forbes 2011), concealment from predators (e.g. Holway 1991, Varpe & Tveraa 2005; but see Hoover & Brittingham 1998), and vantage points over territories (Götmark *et al.* 1995). Identifying whether birds show preferences for certain habitat characteristics, and demonstrating the consequences of these choices, are key concepts in studies of habitat selection (Clark & Shutler 1999, Jones 2001). Ultimately, understanding habitat selection processes and identifying preferred habitat facilitates monitoring and conservation efforts. However, relationships among nesting habitat, breeding success and adult survival remain largely unknown for many birds.

For some bird species there are potential trade-offs associated with the physical characteristics of nest sites. Concealment and shelter may benefit the survival of chicks and adults or provide physiological advantages that improve hatchability of eggs, but may also compromise the detection of predators or other beneficial behaviours (e.g. visual surveillance of territories and resources: Rendell & Robertson 1989, Götmark *et al.* 1995). Cavity nesting by some polar seabirds provides shelter from harsh environmental conditions, but cavities are prone to snow accumulation. Nesting in cavities may provide protection from wind chill and a more favourable microclimate for incubation and chicks (e.g. Hodum 2002, Mallory & Forbes 2011), but for the medium-bodied (250 g to 500 g) Snow Petrel *Pagodroma nivea* obtaining a nest that is not frozen is a key requirement for breeding (Jouventin & Breid 2001). We explored this trade-off at a Snow Petrel colony exposed to moderate snowfall and regular strong winds. A two-year study provided the opportunity to compare habitat selection and productivity in different weather conditions. We hypothesised that well-sheltered cavities out of the wind would be used for breeding — assuming that increased shelter provides more stable temperatures (Hodum 2002, Mallory & Forbes 2011) and energetic benefits (Weathers *et al.* 2000) — but would be subject to reduced breeding success due to higher rates of ice accumulation (as in Chastel *et al.* 1993).

METHODS

All nests were located on Béchervaise Island (67°35′S, 62°49′E), approximately 2 km northwest of Mawson Station, in Mac. Robertson Land, East Antarctica. Past surveys identified over 200 cavities with an entrance large enough to be accessed by Snow Petrels, and some were the site of successful breeding by the small Snow Petrel size morph (subspecies *nivea*) (Southwell *et al.* 2011).

Cavity occupancy and breeding success

A total of 120 cavities judged large enough (by entrance size) to be accessed by Snow Petrels — thereby considered "available" — were monitored during the 2009/10 and 2010/11 breeding seasons. Snow Petrels show high fidelity to their nesting site (Jouventin & Breid

2001) but are well known to skip breeding even among the most productive pairs (Chastel *et al.* 1993, Olivier *et al*. 2005), and thus we monitored nesting cavities over two successive years. Cavities were checked every 2 to 3 days to determine the presence of adults, an egg, or a chick, from late November until mid-February to assess three breeding parameters: occupancy (the proportion of cavities occupied), laying success (the proportion of cavities with eggs from occupied cavities) and breeding success (the proportion of chicks at mid-chick-rearing) (nominally 14 February at Béchervaise Island, Fig. 1) from all nests with eggs. Nests were considered occupied when an adult was sighted on at least one occasion. Because some cavities were deep, we used a burrowscope (wireless inspection camera 9 mm with four LED lights). Cavities were deemed unavailable if they were completely inundated by ice through until late incubation. In 2010/11 eight cavities were unavailable, so an additional eight new cavities were monitored for robust inter-year comparisons.

Nest site and cavity characteristics

Characteristics of 128 cavities were measured in late February 2011 using a set of 11 descriptors and an additional two descriptors (slope and aspect) for the surrounding 10 × 10 m area (Table 1). Cavity characteristics included nest type, number of entrances, and entrance orientation (to the nearest degree) measured with a handheld GPS (Garmin eTrex). Physical characteristics (± 1 cm) included depth, entrance height and width, nest chamber volume, and narrowest tunnel size measured using a 5 m tape measure. Nest bowl characteristics included "slope," "substrate" and the presence of "ice" in the nest bowl through egg laying and incubation (Table 1). Slope and aspect for each cavity were obtained from the spatial analyst extension of ArcGIS (ESRI 2002) by generating a 5 m resolution elevation surface in ArcInfo from contour lines and spot heights.

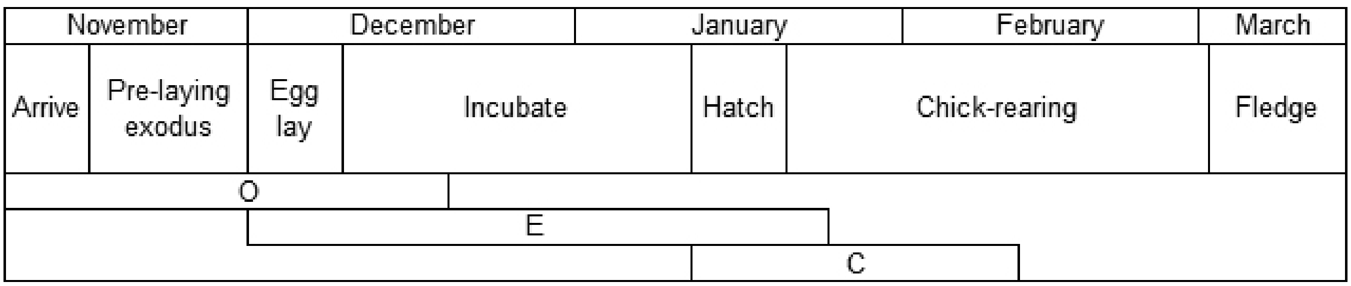

Fig. 1. Calendar summarising the breeding chronology of Snow Petrels at Béchervaise Island during the two year study period (2009/10 and 2010/11), as well as the timing of data collection to assess occupancy (O), laying success (egg presence – E) and breeding success (chick presence – C).

TABLE 1
Variables recorded for each cavity including the characteristics of the surrounding site, the cavity entrance and the nest bowl

Variable	Description
Site	
Slope	F = flat (0°); LS = low slope (1°–5°); MS = moderate slope (5°–20°); Steep slope (20°–45°)
Aspect	North = 314°–45°, East = 46°–135°, South = 136°–225°, West = 226°–315°
Nest type	1 boulder, >1 boulder, in a crack, under a slab
Cavity entrance	
Entrance	1, or >1
Orientation	Mid-point of the nest entrance (degrees)
Width	Maximum width of cavity entrance (cm)
Height	Maximum height of cavity entrance (cm)
Nest bowl	
Minimum tunnel size	Height × width at narrowest point along tunnel (cm^2)
Depth	Maximum length, outside edge of entrance to centre point of nest bowl (cm)
Chamber volume	Maximum height × depth × width from the mid-point of the nest bowl (cm^2)
NBSlope	Flat = 0°, Moderate slope = 1°–5°, Steep slope = 5°–10°
Substrate	Rock slab, large gravel, fine gravel
Ice	Absent, present

Data analyses

An initial univariate analysis of disproportionate prevalence of cavity characteristics — considered evidence of nest selection (as in Clark & Shutler 1999, Keating & Cherry 2004) — was assessed by combining the two years of observations. Cavities were classed as: E – breeding sites with an egg laid in one or more years, O – non-breeding sites occupied but no egg laid in either year, or U

TABLE 2
Variables describing characteristics measured at cavities that were used for breeding (egg laid in at least one year), non-breeding (but occupied in at least one year) or unused by Snow Petrels at Béchervaise Island

Variable	Breeding	Non-breeding	Unused
	n = 94 sites	n = 27 sites	n = 7 sites
Site			
Slope (%)			
Flat	8.2	2.9	7.1
Moderate	14.3	20.6	14.3
Steep	77.6	76.5	78.6
Aspect (%)			
North	40.8	35.3	14.3
East	7.1	8.8	7.1
South	37.8	32.4	50.0
West	14.3	23.5	28.6
Nest type (%)			
1 boulder	44.9	50.0	28.6
>1 boulder	13.3	11.8	21.4
Slab	24.5	23.5	35.7
Crack	17.3	14.7	14.3
Cavity entrance			
Orientation (%)			
North	29.6	26.5	21.4
East	26.5	41.2	35.7
South	19.4	20.6	14.3
West	24.5	11.8	28.6
Entrance (% 1 entrance)	76.0	45.8[a]	85.7
Entrance height (m, mean ± SE)	0.31 ±0.42	0.26 ±0.15	0.21 ±0.09
Entrance width (m, mean ± SE)	0.70 ±0.48	1.11 ±0.60[c]	1.00 ±0.71
Nest bowl			
Nest bowl slope (%)			
Flat	86.7	52.9[c]	64.3
Moderate	13.2	41.2[c]	21.4[c]
Steep	0.0	5.9	14.3[a]
Substrate (%)			
Bare rock	7.1	26.5[b]	42.9[c]
Gravel	38.8	29.4	21.4
Sand	54.1	44.1	35.7
Minimum tunnel size (m^2, mean ± SE)	0.088 ±0.153	0.164 ±0.161[c]	0.086 ±0.057
Depth (m, mean ± SE)	0.96 ±0.61	0.90 ±0.40	0.69 ±0.34
Chamber volume (m^3, mean ± SE)	0.026 ±0.039	0.047 ±0.052[b]	0.020 ±0.017

Binomial tests (showing chi-square) for categorical characteristics and Mann-Whitney U tests for measured nest and nest bowl characteristics compare the differences between egg laid versus occupied, and occupied versus unoccupied: [a]$P < 0.05$, [b]$P < 0.01$, [c]$P < 0.001$.

– unused in both years. To account for non-parametric and unequal variances, Mann–Whitney U tests were used to compare E versus O and E versus U, and binomial tests were applied to habitat variables measured as proportions.

Second, a staged modelling approach was applied to each stage of breeding (occupancy, egg-laying success, chick-breeding success) within breeding seasons to identify whether characteristics of cavities resulted in increased use or reproductive output in that year. Logistic regression models were used with a binomial error distribution applied using generalised linear models (GLMs) (as in Velando & Freire 2003, Bourgeois & Vidal 2007). Models for the response variables "occupancy," "egg" and "chick" were constructed with characteristics of the site, cavity entrance and nest bowl (Table 1) used as explanatory variables. Models were constructed for each year to account for changes in ice accumulation with weather conditions. Where multi-colinearity occurred between habitat variables, the least directly relevant variable was omitted, and ecologically meaningful interactions (i.e. that made sense) were included but kept to a minimum to avoid over-parameterisation of models (Burnham & Anderson 2002).

For all models, habitat variables were included in a full model and terms removed until a minimum adequate model was determined, following Crawley (2005). Briefly, the order of deletion of terms was determined from chi-square tests for full models and reduced models in which only that single term had been deleted. Significant terms were retained, and the removal of other terms was repeated until all terms in the model were statistically significant at $P \leq 0.05$. When each explanatory variable was removed in turn, the difference in percent deviance explained identified its comparative value in explaining the observed variation in the response variable: occupancy, egg, or chick. Over-parameterisation due to a reduced number of nests with eggs laid was avoided for the chick model by identifying the most significant terms in two initial models including a subset of parameters (1 – nest entrance and nest bowl characteristics, 2 – nest bowl and site characteristics; Table 1). The most relevant terms from these sub-models were then included in the final model. Significance levels were established at $P < 0.05$, and we report means ± standard deviations. All statistical analyses were performed using R v.2.11.0 (R Development Core Team 2008).

Weather conditions

To identify the role of local weather on patterns of occupancy, laying success or chick survival, we used wind direction and wind speed collected 3 km away at Mawson Station (assumed to reflect conditions at the study site). Wind data were provided by the Australian Bureau of Meteorology (www.bom.gov.au) and were collected throughout the field season. Daily averages of wind direction and wind speed were calculated from measurements every three hours; averages are presented in wind rose plots.

RESULTS

There was no evidence of surface nesting at the study site or in the broader Mawson region as all eggs were laid either in cracks or under boulders and slabs. A similar proportion of cavities was occupied in 2009/10 (84.9%) and 2010/11 (85.6%), but laying success was lower in 2009/10 (57.4%) than 2010/11 (67.3%). Despite reduced egg laying in 2009/10, breeding success was higher (56.9%) than during 2010/11 (32.4%). Of the cavities accessible by Snow Petrels in both years (n = 112), only 35.2% had breeding ("egg") in both years, while 26.6% were unoccupied (i.e. never used) despite being perceived to be "available." Breeding pairs skipped breeding (egg laid in one year and occupied in the other year) in 35.0% of nests, assuming these nests had been retained by the same breeding pairs.

Univariate comparisons of nest use revealed that the majority of unused cavities sloped moderately or steeply, or did not contain any loose substrate (Table 2). There was higher occupancy of cavities with flat nest bowls, and most breeding occurred on flat nest bowls that contained loose substrate (gravel or sand) (Table 2). Modelling

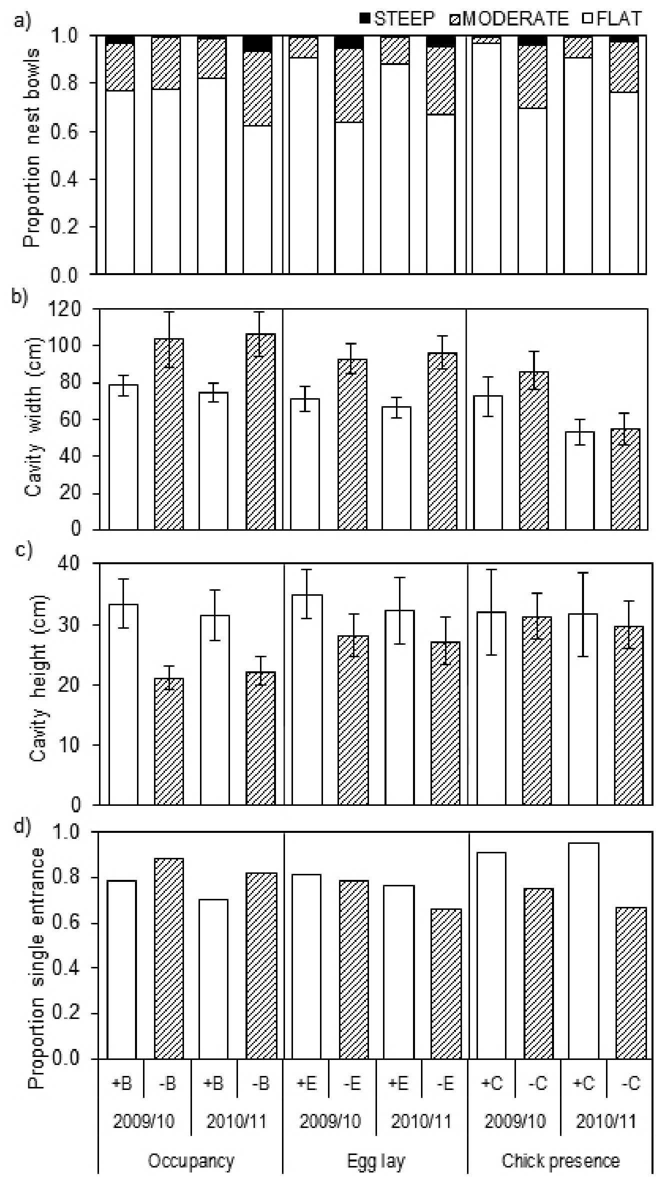

Fig. 2. Physical cavity characteristics significantly correlated with stages of nest use in Snow Petrels: a) slope of nest bowl; b) width at entrance; c) height at entrance; and d) number of entrances, showing nest occupancy (containing a bird, +B), egg laying (containing an egg, +E), and chick survival (containing a chick, +C). Note: proportion of single entrances reflects the proportion of nests in a category (e.g. +E) with single entrances as compared to the remainder with multiple entrances.

concurred, as egg laying was significantly correlated with nest bowl slope in both years (Table 3) — eggs were more frequently laid in flat nest bowls (Fig. 2a). Chick survival significantly correlated with nest bowl slope in 2009/10, with reduced survival in sloping bowls (Fig. 2a). Cavity usage was also correlated with nest chamber size and nest bowl substrate, but to a lesser extent, and these characteristics were not retained in models with stage of breeding or between years (Table 3).

The majority of cavities with eggs laid had single entrances (Table 2), significantly narrower entrances and tunnels, and smaller nest chambers compared with occupied cavities with no egg laying (Table 2). Modelling results in 2010/11 confirmed that cavities with narrower entrances had a higher rate of occupancy (Table 3, Fig. 2b), and egg laying (Table 3, Fig. 2b). Interestingly, a greater proportion of cavities with higher entrances were occupied compared with cavities with low entrances (Fig. 2c). Egg laying in 2010/11 and chick survival in both years were correlated with the number of entrances (Table 3): eggs were laid more often and chicks survived better in single-entrance cavities than in those with multiple entrances (Fig. 2d).

Modelling revealed that cavity use was not correlated with steepness of the surrounding area (Table 3), but occupancy and egg laying in 2009/10, and occupancy and chick survival in 2010/11, were significantly correlated with aspect (Table 3). Correlations between nest use and aspect varied through stages of breeding, as cavities on aspects with high occupancy did not always have high laying success or chick survival (Fig. 3a). The correlation between nest usage and aspect also varied between years (Fig. 3a, Table 3) coinciding with changes in weather and ice accumulation. In 2009/10, when southeasterly winds predominated in the months before breeding (Fig. 4a), ice accumulation occurred only in cavities on northern and western aspects (Fig. 3b), i.e. the lee side of the island. Consistent southeasterly winds may also have contributed to the complete failure of cavities on easterly aspect (Fig. 3a). In contrast, in 2010/11, winds were more variable, with some southerly and westerly winds (Fig. 4b), and the number of strong wind days (daily average wind speed >15 km/h) was higher (Fig. 4b). Stronger, more variable winds corresponded with more widespread ice accumulation in 2010/11 (Fig. 3b), with more cavities on northern and western aspects having ice than during the previous year. Even cavities on eastern and southern aspects that were clear the previous year accumulated ice in 2010/11 (Fig. 3b). Due to a southeasterly ridgeline on Béchervaise Island, north and south aspects predominated, and the island thus contained a larger proportion of cavities on these aspects (Fig. 5).

Modelling revealed that cavity occupancy was significantly correlated with ice accumulation in both years, and egg laying

TABLE 3
Generalised linear models for selection of specific characteristics with stage of breeding by Snow Petrels on Béchervaise Island in 2009/10 and 2010/11, assuming a binomial distribution of errors and a logistic link

	Change in deviance, year					
Stage	**Occupancy**		**Egg**		**Chick**	
Variable[a]	**2009/10**	**2010/11**	**2009/10**	**2010/11**	**2009/10**	**2010/11**
Site						
Aspect	22.7^{c}		7.2^{c}			
Nest type			3.9^{b}			
Cavity entrance						
Number of entrances				3.7^{b}	7.9^{c}	4.5^{b}
Width at entrance	8.2^{c}	7.8^{c}		6.1^{b}		4.8^{b}
Height at entrance	11.6^{c}	7.1^{c}			5.6^{b}	
Depth	5.0^{b}					
Nest bowl						
Volume of chamber	4.1^{b}					4.1^{b}
Nest bowl slope		13.5^{c}	13.2^{c}	6.5^{b}	9.3^{c}	
Nest bowl substrate					6.2^{b}	
Tunnel size (min)	5.7^{b}				7.4^{c}	
Ice	4.9^{b}		8.8			
Ice × Aspect		11.5^{c}				4.0^{b}
Residual deviance	56.6	59.9	63.6	76.1	68.7	80.9
Degrees of freedom	110		100		57	

[a] The "occupancy" model included all cavities, the "egg" model included the subset of cavities that were occupied, and the "chick" model the subset of cavities in which eggs were laid. The remaining variables (see Table 1) were not significant.
GLM: $^{b}P < 0.01$, $^{c}P < 0.001$.

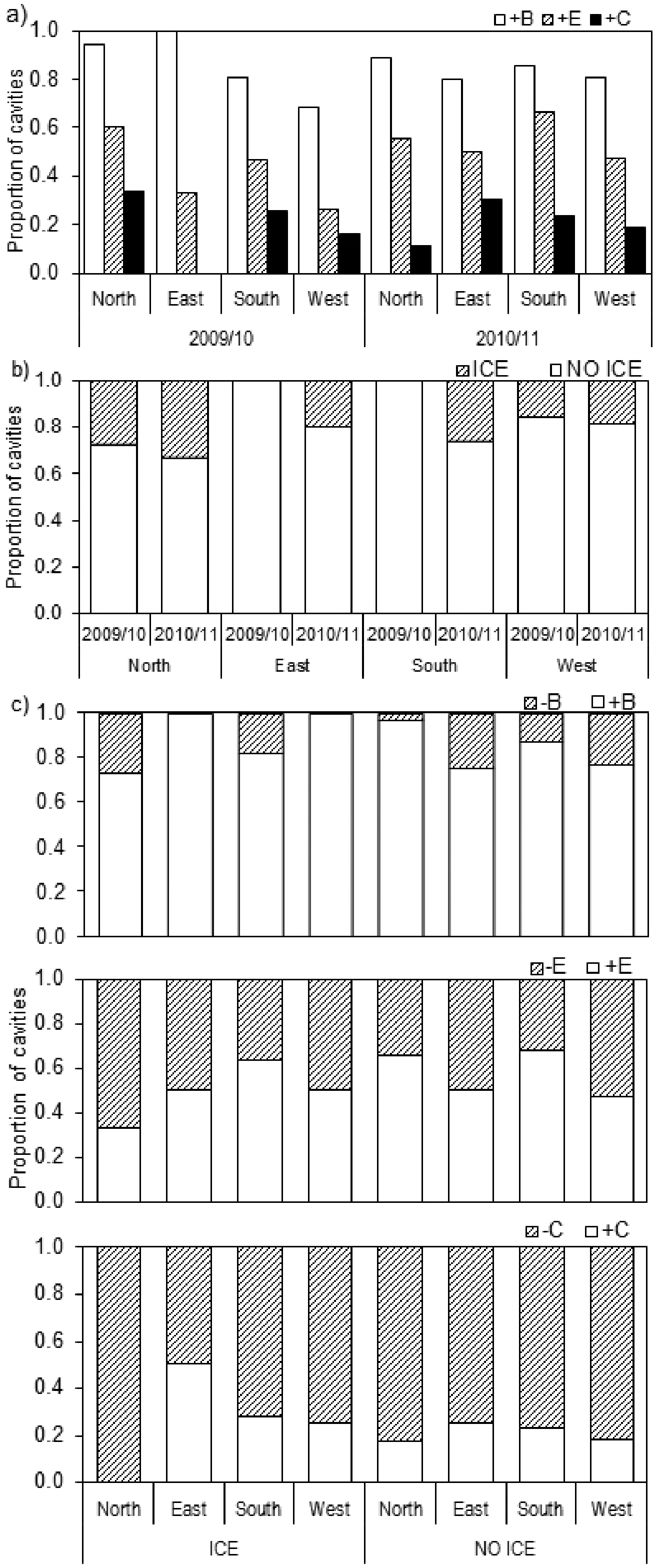

Fig. 3. Inter-annual variation in a) ice accumulation in cavities across all aspects; b) varying effect of ice on occupancy, egg lay and chick survival with aspect for 2010/11; and c) the proportion of cavities occupied (containing a bird, +B), containing an egg (+E) and containing a chick (+C) across all aspects. Note: The different sample size of nests between aspect categories reflects the uneven spread of cavities across aspects (i.e. more cavities on north- and south-facing slopes than on east- and west-facing slopes).

correlated with ice accumulation in 2009/10 (Table 3). The significant interaction term Ice × Aspect in the most supported models of 2010/11 reveals that the effect of ice varied with aspect (Table 3). In 2010/11 all eastern and western cavities containing ice were occupied, whereas only two-thirds of northern cavities containing ice were occupied (Fig. 3c). In 2010/11, ice affected egg laying (Table 3), as eggs were laid in a similar proportion of cavities with and without ice (50% vs. 61%, respectively). On northern slopes, no chicks from eggs laid in iced cavities survived, whereas on eastern slopes chick survival in iced nests was high (Fig. 3c), indicating that accumulation was more extensive on northern slopes.

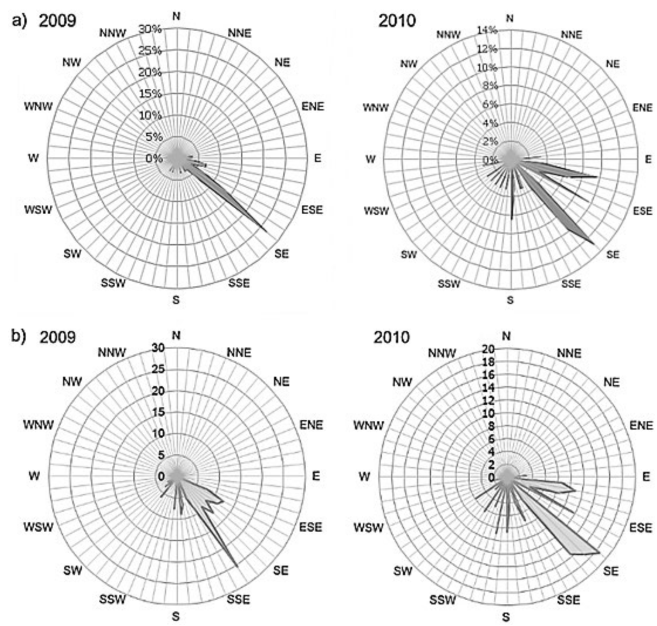

Fig. 4. Inter-annual variation in wind conditions (wind rose plots) at Mawson Station for the 2 month period that overlapped with nest occupancy and egg laying (November and December), showing a) proportion of daily winds from each directional category (degrees), and b) average daily wind speed (km/h) from each directional category (degrees).

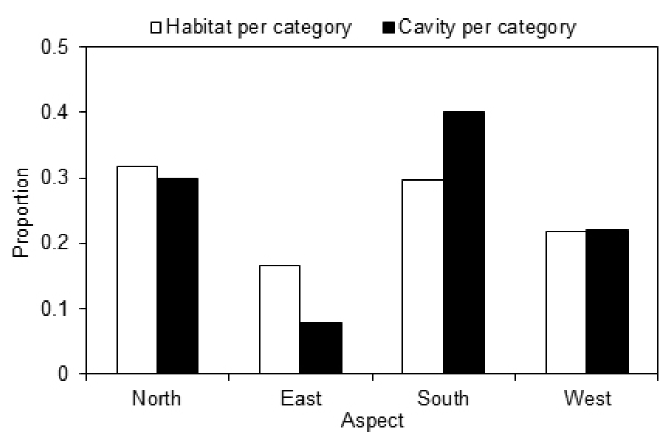

Fig. 5. Distribution of aspect available on Béchervaise Island as a proportion of 10 × 10 m grid cells assigned to each category (by the Digital Elevation Model using GIS) and the aspect of the cavities studied.

DISCUSSION

We show that Snow Petrels at Béchervaise Island do not use cavities for nesting randomly. Rather, there was disproportionately higher use of cavities with single and narrower entrances, and a flat nest bowl. Acquiring a more sheltered nest increased the chances of nest success, presumably by reducing the risks of failure due to inclement weather or predation by South Polar Skuas *Stercorarius maccormicki*. Presumed benefits of a single narrower entrance is reduced air flow, which brings increased shelter. However, this was not measured. Hodum (2002) demonstrated that cavities provide protection from wind chill and more stable temperatures for Snow Petrels than open ground. In polar environments, though, sheltered and deep nests may also be colder than sites exposed to solar radiation (Mallory & Forbes 2011), evidenced by the retention of snow and ice in cavities long after they have melted from exposed areas. For the cliff- and cavity-nesting Northern Fulmar *Fulmarus glacialis* in the Arctic, cave entrance size and overall shelter are also positively related to nest usage and productivity (Mallory & Forbes 2011).

Exclusive cavity nesting by Snow Petrels in the Mawson region further demonstrates that sheltered sites are important to successful breeding. Cavity nesting is most common in other parts of Antarctica (Ryan & Watkins 1989, Chastel *et al.* 1993, Hodum 2002, Tveraa & Christensen 2002); however, there are colonies where some, or all, Snow Petrels are surface nesters (Goldsworthy & Thomson 2000, Jouventin & Breid 2001). Is the availability of cavities driving this varied nesting habit? Or do milder weather conditions (i.e. lee side of mountains) and lower predation pressure preclude the need to seek shelter and concealment in cavities? And what are the reproductive consequences of cavity nesting versus surface nesting? Broadening our study across a range of colonies, in combination with an assessment of nest microclimate (as in Kim & Monaghan 2005, Mallory & Forbes 2011) and associated thermoregulatory costs to adult and chick (Weathers *et al.* 2000) would provide greater insight into the drivers of nesting behaviour and the fitness consequences in this species.

Results from our staged modelling (through stages of breeding) revealed that shelter characteristics were important during occupancy whereas features of the nest bowl were more important for egg laying and chick survival. Egg laying was directed at cavities with a low angled internal surface and nest bowls containing sand or gravel. These characteristics enabled the formation of a suitable bowl. The value of a nest-bowl has been demonstrated for some surface nesting seabirds (e.g. Kelp Gull *Larus dominicanus* García-Borboroglu & Yorio 2004) and ledge nesters (e.g. Thick-billed Murres *Uria lomiva*, Birkhead *et al.* 1985), but is often overlooked in nest-use studies of cavity nesters (e.g. Stokes & Boersma 1998, Velando & Freire 2003, Bourgeois & Vidal 2007, but see Cairns 1980, Bolton *et al.* 2004). For Snow Petrels at Béchervaise Island nest-bowl characteristics improved laying success and chick survival, presumably by retaining eggs and minimising chick falling risk. Characteristics of the nest bowl affect Snow Petrel productivity consistently across all regions, as a round egg cannot be retained on a sloping surface. Due to the importance of egg retention in successful breeding, an initial assessment of nest bowl slope can provide a useful first pass to identify the most viable breeding sites.

Nest quality is best demonstrated when birds occupy nests with features that pertain to egg and chick survival later in the breeding season (Martin 1998, Jones 2001). Accordingly, several Snow Petrel nest characteristics were retained in models through multiple stages of breeding (entrance width, entrance height, nest bowl slope). We infer that nest cavities with smaller entrances and flat nest bowls provide better-quality nests for Snow Petrels owing to their higher rates of egg retention and chick survival. However, there is no guarantee that the presence of individuals in a given habitat or their breeding performance is positively related to habitat quality. Further studies are required to demonstrate how the physical characteristics of Snow Petrel nests can influence microclimate (e.g. Weathers *et al.* 2000, Kim & Monaghan 2005) and thereby influence parental behaviour at the nest (e.g. Fast *et al*. 2007, Mallory & Forbes 2011).

We document the overwhelmingly negative effect of ice accumulation on Snow Petrel breeding. Chastel *et al.* (1993) also demonstrated this relationship, reporting reduced annual productivity of a colony when more nests contained ice. Snow and ice in nest cavities reduce their thermal capacities and increase the chance of melting and refreezing ice (Chastel *et al.* 1993, Jouventin & Breid 2001). Our study demonstrated the expected trade-off between shelter and ice accumulation and the role of local weather. In years of low snowfall, sheltered nests on the lee side of the island may benefit breeding, but in years of high snowfall or windblown snow, sheltered cavities are more prone to ice accumulation. This occurred on Béchervaise Island in 2010/11, as sheltered cavities with a higher rate of egg laying were more prone to ice accumulation and breeding failure, although not all iced nests failed. Similarly, for the surface-nesting Adélie Penguin *Pygoscelis adeliae,* nesting in the lee of topographical features provides shelter from wind and weather, but these sites accumulate more snow during storms, resulting in nest failure (Trivelpiece & Fraser 1996, Bricher *et al.* 2008). Cavity-nesting Arctic seabirds (e.g. Guillemots, Auklets and Razorbills *Alca torda*) and surface-nesters that nest among boulders (e.g. Puffins and Northern Fulmars) may experience a similar trade-off, as snow accumulation from heavy snowfall and blizzards is known to reduce breeding success in a range of species (Mallory *et al.* 2009). Where future climate changes include increased snowfall and winds, we predict a decrease in Snow Petrel productivity as more widespread ice accumulation of nesting cavities will limit their value as a breeding site, as has been the case for Adélie Penguins (Trivelpiece & Fraser 1996, Patterson *et al*. 2003).

ACKNOWLEDGEMENTS

We are grateful to the Mawson Station leaders Mike "Duk" Craven and Jim "Chippie" Milne, and many unnamed Mawson personnel for their logistical support and assistance with field work. Many thanks to Susan Doust for assistance with data collection. This project complies with the laws of Australia, was carried out with approval from the Australian Antarctic Division's Antarctic Animal Ethics Committee, and was supported by the Australian Antarctic Division ASAC project #2722. We appreciate the help from two anonymous reviewers.

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