NEST CONCEALMENT AND ITS RELATIONSHIP TO PREDATION AND REPRODUCTIVE SUCCESS IN THE MAGELLANIC PENGUIN AT ITS SOUTHERN-MOST CONTINENTAL COLONY

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Abstract. This paper analyses the effects of nest-site characteristics on reproductive success of the Magellanic Penguin (Spheniscus magellanicus) during five breeding seasons at Cabo Vírgenes (52°20′S, 68°21′W) on the Patagonian coast of Argentina. During three out of five breeding seasons egg losses were lower in nests with high cover than in low cover. Mean fledging success was greater in high than in lower cover nests. An experiment performed with abandoned eggs placed in empty penguin nests showed: 1) Eggs placed in nests with high cover were less likely to disappear than those in nests with little cover, 2) Egg losses were higher in nests located in peripheral areas than in central ones, and 3) Egg losses were lower in nests with high cover than low cover in both central and peripheral areas. Most nests were orientated against prevailing winds. Our results suggest Magellanic Penguins are selecting nest entrances to minimize heat loss and to reduce their energy budget. We designed a nest quality index with the variables interpreted as important by a multivariate analysis (Principal component analysis). The result showed that the most successful nests were situated under tall bushes with high cover at the roof and to the south and were located close to other nests. This could be the result of an anti-predation strategy where the prey selects concealment of the nest in preference to self-defense against predators. Accepted 9 April 1999.

Key words: Cabo Vírgenes, Magellanic Penguins, Spheniscus magellanicus, nest site, predation, reproductive success.

INTRODUCTION

Nest sites are a critical resource for most birds during the breeding season. Nests should be placed at locations which minimize predation and provide adequate microclimate conditions to avoid high metabolic costs to adults and chicks. Nest cover affects breeding success in many bird species (Rodenhouse 1986, Martin & Roper 1988, Walsberg 1985) including penguins (Seddon & Davis 1989, de Bary Pereda 1990, Frere *et al.* 1992). Protection of eggs and chicks from predators

depends on nest quality (Hudson 1982, Martin & Roper 1988, Seddon & Davis 1989) including nest orientation (Austin 1976), nest height (Rendell and Robertson 1989) and, in colonial species, location within the colony (Tenaza 1971, Frere et al. 1992, Emslie et al. 1995). The effect of nest cover on the breeding success of the Magellanic Penguin (Spheniscus magellanicus) was previously studied in a colony (Punta Tombo) located approximately 1000 km north of our study area by de Bary Pereda (1990), Frere et al. (1992) and Stokes and Boersma (1998), where annual changes

in breeding success are mainly determined by food availability (Boersma *et al.* 1990). This paper analyses how nest site characteristics affect breeding success at its southernmost continental colony, where extremes in weather conditions limit breeding success in penguins, causing high nest desertion rates and chick mortality (Frere *et al.* 1998).

STUDY AREA, NEST SITES, AND BREEDING CYCLE

Cabo Vírgenes is the southern-most continental Magellanic Penguin colony, located in Santa Cruz province (52°20'S, 68°21'W) and the second largest in Argentina with approximately 90,000 breeding pairs (Gandini et al. 1996). Magellanic Penguins use nest sites such us natural crevices, places under bushes or burrows (Gandini 1993). Burrows are those nests where all or most the protection is given by a soil roof and soil walls, bush nests are those where the shrub's foliage or branches provide all or most of the protection (de Bary Pereda 1990). Topography and soil are determinant of the location and type of nests constructed by Magellanic Penguins (Capurro et al. 1988). In contrast to other penguin colonies along the Argentine patagonian coast, Magellanic Penguins at Cabo Vírgenes nest only under bushes (Lepydophilum cupressiforme) (Gandini 1993). Only densely vegetated areas are chosen for breeding (Gandini et al. 1997). Magellanic Penguins lay two eggs which are incubated by both parents. Similarly to other penguin colonies at Cabo Vírgenes, predation is highest during incubation and the first week after hatching (Frere et al. 1996). The main predator on eggs and young chicks at this colony is the Kelp Gull (Larus dominicanus) (Frere et al. 1996).

METHODS

We gathered information on breeding activi-

ties and reproductive success of marked individuals at marked nests in several study areas within the colony from 1989 to 1993 (see Gandini *et al.* 1997).

We sampled 145, 143, 143, 120 and 106 active nests during the 1989, 1990, 1991, 1992 and 1993 breeding seasons. We checked nests daily from September, the beginning of the breeding season, until early November, after eggs had been laid. In late November when chicks started hatching, daily nest checks continued until fledging which occurred as late as mid-January. At each visit we recorded number of eggs, chick and egg losses, and fledging success (number of fledglings by nest) . The amount of vegetation covering bush nests varies from nearly none to complete. We classified bush nests as having either more, or less than 50% vegetative cover over the nest cup (Frere et al. 1992). We compared the number of eggs laid in each of the two nest categories defined above. The number of breeding seasons a nest was used ("Nn") and its fledging success in each year were determined, together with the mean fledging success for the five year study. We considered a chick to have fledged if it was alive in mid January and if it weighed at least 1.8 kg (Boersma et al.

At each study nest we measured: 1) height and width of the nest entrance, 2) the amount of cover from the bush at the roof of the nests and on all four sides of the nest (North, South, East and West), 3) nest entrance orientation, 4) the height and width of the bush and, 5) the distance to the nearest nest. Roof cover was measured looking at the nest cup from directly above the nest. When the bushes were taller than the observer we used a step ladder to make the roof measurements. The amount of cover on each of the four sides as determined by compass directions was estimated to the nearest 5%. Nest orientation was measured with a hand-held compass and grouped in eight categories to

TABLE 1. Number of active nests, number of laid eggs, and percent of egg losses in high cover nest
(> 50%) and low cover nests (< 50%) during the study period at Cabo Vírgenes colony.

Breeding seasons	High cover (> 50%)			Low cover (< 50%)		
	No. of active nests	No. of laid eggs	Percent of lost eggs	No. of active nests	No. of laid eggs	Percent of lost eggs
1989–1990	63	162	17	82	124	20
1990–1991	71	135	65	72	137	80
1991–1992	71	138	26	72	137	44
1992–1993	59	114	15	61	118	24
1993–1994	59	114	8	47	91	18

use Chi-square goodness of fit for circular data (Zar 1984). Nest orientation was also assigned one of four categories (North, South, East and West) to compare frequencies wind flows in each direction with frequencies of nest entrances.

Principal component analysis (PCA) was used to identify which of the following factors explained the variation among nests: 1) cover provided by the roof and side cover at each of four compass directions, 2) bush width and height, 3) nest entrance height and width, and 4) nearest neighbor distance. We retained only factors with eigenvalues greater than one (Cooley and Lohmes 1971). We transformed the percentage variables using the arcsine transformation.

During one breeding season (1990), we performed an experiment to evaluate the effects of nest cover and nest location within the colony on egg detection by predators. We collected abandoned eggs from outside the study areas and placed one egg in one of four categories of nests mentioned below during the incubation period. Nest types were classified by its bush cover and position in the colony as: 1) high cover (> 50%), 2) low cover (< 50%), 3) central nests 4) peripheral nests. We considered a nest placed in a central area if it was surrounded by other nests, and peripheral when nests only have neighbors on

one side. Sixteen single eggs were placed in "high cover" nests and sixteen in "low cover" nests. We also chose sixteen empty nests with similar cover in a central area and sixteen empty nests in a peripheral one and measured egg loss. We checked each nest every 12 h. for one week or until the egg disappeared. All nests where a penguin was attending the egg when we visited were excluded from the analysis. To understand the simultaneous effects of cover and nest location we used Cochran's Q-test of dichotomous variables to test differences in egg loss using 130 chosen active nest out of the study areas. The four nestquality classes were high-cover central (N = 42), high-cover peripheral (N = 32), lowcover central (N = 24) and low-cover peripheral (N = 32).

RESULTS

Nest cover, predation and fledging success. Clutch size was similar in nests with low cover (< 50%) vs high cover (> 50%) over all the study period ($\chi^2_{89-90} = 0.06$, df = 1, P = 0.8; $\chi^2_{90-91} = 0.06$, df = 1, P = 0.8; $\chi^2_{91-92} = 0.12$, df = 1, P = 0.73; $\chi^2_{92-93} = 0.75$, df = 1, P = 0.10; $\chi^2_{93-94} = 0.09$, df = 1, P = 0.75).

During three out of five breeding seasons egg losses were significantly greater in nests with less than 50% roof cover, $(\chi^2_{89-90} = 0.21,$

df = 1, P > 0.05; $\chi^2_{90-91} = 7.14$, df = 1, P < 0.05; $\chi^2_{91-92} = 9$, df = 1, P < 0.05, $\chi^2_{92-93} = 2.35$, df = 1, P > 0.05, and $\chi^2_{93-94} = 7.14$, df = 1, P < 0.05; Table 1). Even in those years where differences where not statistically significant predation was higher in "low" cover (< 50%) nests than in "high" cover (> 50%) nests (Table 1). Mean fledging success of each nest was higher in "high" cover nests (mean = 0.74, SD = 0.05, N = 134) than in "lower" cover nests (mean = 0.59, SD = 0.04, N = 161; Kruskal-Wallis ANOVA, H = 5.043, P = 0.024). The number of breeding seasons a nest was used ("N_n") was positively associated with roof cover (Mann-Whitney U-test, U = 0.20, N = 295, P = 0.0006).

The egg experiment indicated that eggs placed in nests with high cover were significantly less likely to disappear than those in nests with little cover. In nests with "low" cover, eggs were preyed upon within 24 h (mean = 22.9 h, SD = 3.62 h, N = 11), while in nests with "high" cover some eggs remained for a week (mean = 54.54, SD = 42h, N = 11), (Mann-Whitney U-test, z = 2.67, P = 0.0078), suggesting eggs may have remained undetected, by aerial predators. The comparison between central and peripheral nests showed that egg loss was significantly lower in central than in peripheral nests (χ^2 = 4.133 df = 1, P < 0.05, N = 32). Predation was also higher in central and peripheral low cover active nests (Cochran's test, Q = 21.14, df = 2, P = 0.0002).

Nest site characteristics. Orientation of nest entrance was not randomly distributed (χ^2 = 59.33, df = 7, P < 0.0001). Most nest entrances were orientated away from the prevailing wind directions (r_s = -0.98, N = 291, P < 0.0001, Fig.1.).

First, second, and third PCA components of nest characteristics explained 26%, 13% and 11%, respectively, of total variance. To interpret these axes we considered loadings

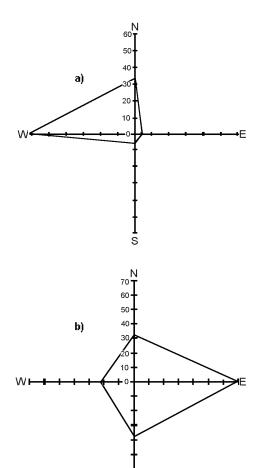


FIG. 1. a) Prevailing winds during the breeding season of Magellanic Penguins, at Cabo Vírgenes, Santa Cruz Argentina. Values are the percentage of days during which the wind flows in each direction; b) Nest entrance orientations. Values are the percentage of nest entrances facing in each direction.

greater than 0.70. Thus the first factor grouped nests with more cover at the roof and to the south (loadings 0.74 and 0.72 respectively), the second factor grouped these nests under tall bushes (loading 0.77), and the third factor grouped nests located in low density areas (loading - 0.70).

We designed a nest index with the variables interpreted as important by the first, second and third axis of the principal component defined as $I_n = (R + S + A)/DVC$ where R = roof cover, A = bush height, S = cover at south and, DVC = nearest neighbor distance. We expected that large bushes with dense vegetation would have high nest quality, while nests with high nearest neighbor distances would have low nest quality. Nests with high index values were on average more successful $(r_s = 0.12 \text{ ; } N = 274; P < 0.05)$. High indices were also related with the number of breeding seasons a nest was chosen for breeding $(r_s = 0.16; N = 274; P < 0.01)$.

DISCUSSION

In Magellanic Penguin colonies with bush nesting habitat, bush variability seems to be important in the reproductive output. This study demonstrates that nest concealment affect visibility of the nest to aerial predators. Roof cover is known to provide protection from aerial predators (Frere et al. 1992), more foliage can reduce predator efficiency by increasing the time and number of potential nest sites a predator must search (Martin & Ropper 1988). At Cabo Virgenes where the main predator of penguin eggs is the Kelp Gull (Frere et al. 1996) which generally locates vulnerable eggs by aerial searching, egg losses were consistently low in more protected nests, presumably because gulls have more difficulty finding the nest contents. Both sets of data (study nests and experimental data) suggest that nest cover is a significant determinant of egg retention in Magellanic Penguins even in peripheral areas which experience high predation pressure (Gotchfeld 1980, Frere et al. 1992) and consist of young nesting birds (Tenaza 1971, Gandini et al. 1997). The benefit of cover may be obscured in exceptionally good or poor years, but we find even in those years where differences in egg losses were not statistically significant, data were in the predicted direction; more covered nests suffered less predation.

Nests with greater amounts of cover on the roof and to the south, taller bushes above the nest and centrally rather than peripherally on average, fledge more chicks. The fact that nest entrances face opposite to the direction of prevailing winds is not surprising in a colony where winds can reach 120 km/h (Gandini et al. 1997). At this colony penguins probably select nest sites such that they minimize their own heat loss as well as reduce the energy budget of their chicks.

Pairs breeding in high cover nests fledge in average 20% more chicks each season. Because penguins are long lived seabirds, pairs nesting under high cover nests will have a higher lifetime fitness than those pairs nesting in low cover nests.

In conclusion, at this penguin colony, located near the limit of the geographic distribution of this species, where extreme weather conditions are frequent, and high nest desertion and predation during incubation determine the overall reproductive success of the colony (Frere *et al.* 1998), a particular combination of bush characteristics affects the breeding success. This could be the result of an anti-predation strategy where the prey selects the concealment of the nest as its best defense against predators.

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