

NEST-SITE CHARACTERISTICS AND REPRODUCTIVE SUCCESS IN MAGELLANIC PENGUINS (*SPHENISCUS MAGELLANICUS*)

DAVID L. STOKES¹ AND P. DEE BOERSMA

Department of Zoology, Box 351800, University of Washington, Seattle, Washington 98195, USA

ABSTRACT.—We used cross-sectional, longitudinal, and experimental data to investigate the effects of habitat at the smallest spatial scale—the nest site—on reproductive success of Magellanic Penguins (*Spheniscus magellanicus*). Over an eight-year period, the amount of nest cover was positively correlated with fledging success. The same pairs tended to be more successful when they had more nest cover, and experimental increases and decreases in cover significantly affected survival of nest contents. Other characteristics of nest sites, such as nest type and type of vegetation over the nest, did not affect success. The positive effect of cover resulted mainly from reduced exposure of nest contents to predators during incubation and to high temperatures when chicks were young. Roof cover was positively correlated with fledging success in nests from all areas. Cover on the sides of the nest giving the most protection from the sun was positively correlated with fledging success in warmer sites and with survival of young chicks in all areas. Young chicks at nests with less cover were more likely to move from their nests and to die on hot days. Experimental results indicated that the likelihood of egg detection by predators decreased with increasing nest cover. Height of nest entrance was a significant predictor of egg loss, suggesting that accessibility of nest contents to predators was an important component of predation risk. Thermal properties of nests and risk of predation were related; predation of nest contents was more likely when adults were absent, and during hot weather adults were more often absent from nests with little cover. Although the effect of cover on success was small relative to the large yearly variation in success due to food conditions, cover is likely to influence lifetime reproductive success substantially. Large and long-term data sets and experimental approaches may be necessary to identify subtle but biologically important factors among long-lived organisms that inhabit variable environments. *Received 18 November 1996, accepted 29 May 1997.*

STUDIES OF DIVERSE TAXA have found that an organism's ability to survive and reproduce depends in part on the habitat in which it lives (Smith 1968, Nettleship 1972, Riechert and Tracy 1975, Sargent and Gebler 1980, Swingland 1983, Dobkin 1985). The degree to which a particular habitat influences survivorship or reproductive success is a measure of the relative value of that habitat to the organism. Ultimately, fitness effects resulting from habitat differences are expected to influence the evolution of habitat selection (Levins 1968, Orians and Wittenberger 1991).

Habitat may be defined at various spatial scales (Wiens 1986, Orians and Wittenberger 1991, Bergin 1992), from geographic to microenvironmental. The avian nest site exemplifies habitat at the latter scale, providing a location where adults, eggs, and chicks may be protected from predators (Keppie and Herzog 1978, Martin and Roper 1988) and environmen-

tal stresses (Ricklefs and Hainsworth 1969, Walsberg 1985). The nest site also may offer protection from conspecifics (Finch 1989) and facilitate courtship and pairing (Morse and Kress 1984). Like larger-scale habitat components, nest sites are variable in their characteristics and therefore may differ in their effectiveness at fulfilling one or more of these functions, thus influencing a bird's fitness. Characteristics such as amount of cover (Hudson 1982, Jackson et al. 1988, Martin and Roper 1988, Norment 1993), orientation (Austin 1976), height (Rendell and Robertson 1989), and slope (Birkhead et al. 1985) have been found to influence breeding success. Some studies, however, have found no effect of nest-site characteristics on success (Best and Stauffer 1980, Reitsma et al. 1990, Holway 1991, Howlett and Stutchbury 1996).

Most studies of fitness effects of habitat are based on nonmanipulative cross-sectional data and correlations between habitat characteristics and reproductive success (e.g. Hudson

¹ E-mail: dstokes@u.washington.edu

1982, Birkhead et al. 1985, Rendell and Robertson 1989, Hatchwell et al. 1996; but see Pleszczyńska 1978, Wiens 1985, Howlett and Stutchbury 1996). Although useful as indicators of patterns of success in various habitats, such correlations do not necessarily reveal whether differences in survival or reproductive success are due to the habitats themselves or to attributes of the organisms in them (Coulson 1968, Wooler and Coulson 1977, Pugsek and Diem 1983, Ens et al. 1992). For example, if the individuals best able to raise chicks (e.g. the oldest, most experienced, or largest) also are able to hold the "best" nest sites, then higher success in these sites may simply be a result of the positive correlation between bird quality and apparent nest quality. Confusion of these factors precludes reliable conclusions about the value of habitats to organisms or how organisms select habitats. To understand the forces that drive habitat choices, the relative value of different habitats must be assessed independently of the actual choices individuals make.

In this study we test the essential premise of habitat-selection studies—that habitats differ in ways that affect the fitness of the individuals selecting them—by examining nest-site characteristics and reproductive success in Magellanic Penguins (*Spheniscus magellanicus*) at Punta Tombo, Argentina. We also investigate the mechanisms that account for such effects. To determine if effects are caused by the sites themselves and to avoid confounding bird and site quality, we supplement multivariate and univariate cross-sectional analyses with longitudinal and experimental data. Magellanic Penguins at Punta Tombo are particularly well suited to this approach because of marked variation in nest sites and the opportunity for experimental manipulation of sites, as well as the existence of a long-term data set for a large number of marked individuals and nests.

Magellanic Penguins.—The nest site is the focal point for all terrestrial activities of Magellanic Penguins during their six-to-eight month breeding season. Typically, males begin to claim and defend nest sites in mid- to late September. Females join the males at the nest by early October and produce a two-egg clutch that is incubated alternately by the parents for approximately 40 days. Chicks hatch in mid- to late November and are fed by both parents for 60 to more than 90 days. The chicks are attend-

ed by a parent continuously until they are approximately 30 days old, during which time they usually stay in the nest. Older chicks are usually unattended and sometimes occupy sites away from their natal nest, although they usually return to the nest to be fed. Chicks fledge from mid- to late January through February. After chicks fledge, adults return to their nests to molt before leaving the colony in April.

Penguins at Punta Tombo use nest sites of widely differing types, nesting under bushes (bush nests), in burrows, and occasionally in the open (Boswall and MacIver 1975, Stokes and Boersma 1991). Even among nests of the same type, the amount of cover and other characteristics such as entrance dimensions, orientation, and bush species are highly variable. Because adult penguins at Punta Tombo are subject to almost no terrestrial predation, and death of adults at the colony is rare, any influence of nest quality on fitness should be expressed almost entirely through fledging success. Thus, within a season, differences in fledging success should provide an indication of the relative fitness value of nest characteristics. Most effects of nest characteristics on fledging success should occur in the incubation and early chick-rearing periods, when one-half to more than three-quarters of mortality of nest contents occurs (Boersma et al. 1990, Boersma and Stokes 1995), and when offspring generally are confined to the nest.

Previous results and predictions.—*Spheniscus* penguins are temperate in distribution. Well adapted to life in cold water, they seem over-insulated for life on land (Frost et al. 1976a) and exhibit a wide variety of anatomical, physiological, and behavioral traits believed to be adaptations for survival in warm climates (Stonehouse 1970). Unlike penguins that live in the Antarctic and sub-Antarctic, *Spheniscus* penguins usually nest in sheltered sites (Stonehouse 1967), apparently to avoid direct insolation and resulting high temperatures (Galapagos Penguin [*S. mendiculus*], Boersma 1975; Jackass Penguins [*S. demersus*], Frost et al. 1976a, LaCock 1988). Use of sheltered sites also may reduce predation. Although predation of adults on land is rare at most *Spheniscus* breeding sites, eggs and chicks are subject to many avian and mammalian predators (Boswall and MacIver 1975, Frost et al. 1976b, Yorio and Boersma 1994).

TABLE 1. Characteristics of Magellanic Penguin nests (values are $\bar{x} \pm SD$, with range in parentheses). Sample includes only nests with eggs in 1990. Variables are percent cover on north (NORTH), east (EAST), south (SOUTH), and west (WEST) sides; percent cover on roof (ROOF); average percent cover on all sides (SIDES); height (HEIGHT) and width (WIDTH) of nest-entrance opening; and distance from outside entrance to back of nest (LENGTH).

Variable	Burrow nests ($n = 131$)		Bush nests ($n = 232$)	
NORTH (%)	77.8 \pm 3.41	(0–100)	66.7 \pm 2.41	(0–100)
EAST (%)	80.3 \pm 3.34	(0–100)	56.7 \pm 2.61	(0–100)
SOUTH (%)	71.1 \pm 3.82	(0–100)	66.5 \pm 2.36	(0–100)
WEST (%)	79.1 \pm 3.40	(0–100)	69.6 \pm 2.27	(0–100)
ROOF (%)	96.6 \pm 0.94	(25–100)	77.8 \pm 1.15	(15–100)
SIDES (%)	77.2 \pm 0.68	(45–100)	65.2 \pm 0.74	(0–95)
HEIGHT (cm)	22.3 \pm 0.38	(15–44)	29.1 \pm 0.81	(14–100)
WIDTH (cm)	40.4 \pm 0.78	(26–100)	42.0 \pm 0.68	(22–88)
LENGTH (cm)	68.3 \pm 2.02	(21–131)	83.7 \pm 1.82	(41–200)

These potential selective forces suggest testable predictions to determine whether and how nest characteristics affect reproductive success of Magellanic Penguins. If nest cover significantly reduces the likelihood of heat stress or predation, pairs using nest sites with more cover should have higher fledging success than those in sites with less cover. Roof cover should be particularly important, giving protection from both sun and avian predators. If prevention of heat stress is the primary benefit of cover, birds in nests with less cover on the north and west sides (the sides providing the most protection from the sun in the Southern Hemisphere) and those using nests with the entrance (usually the side of the nest with the least cover) oriented toward the north should have reduced success. If prevention of predation is the major benefit, there should be no particularly favorable compass orientation of maximum side cover.

Characteristics other than amount of cover, such as nest type and bush type, also may be important. Burrows generally provide more cover than bush nests (Table 1); however, even among burrows and bush nests of equal cover, burrows may be advantageous because their thermal properties may be more favorable for chick development (Frere et al. 1992). Nests located under spiny bushes may be better protected against predators than nests under bushes without spines. Because risk of heat stress and predation should vary with changes in temperature and vulnerability of offspring, different nest characteristics may be important at different stages of the breeding season.

Despite ample reasons for expecting nest characteristics to be important determinants of

fledging success, investigations of such effects in Magellanic Penguins have yielded ambiguous results. Gandini (1993) found that different components of nest structure were correlated with fledging success in two years, with no significant correlations in a third year. A nest-quality index was associated with fledging success; however, this index included larger-scale variables (nest density, ambient foliage density, location) in addition to nest characteristics. Specific effects of nest cover have been noted (lower chick mortality in nests protected from wind and rain in an unusually cold year [de Bary 1990], and higher egg predation in nests with very little cover [Frere et al. 1992, Gandini 1993]); however, these effects did not significantly influence fledging success. Frere et al. (1992) found no difference in success at burrows and bush nests despite substantial differences in average cover between the two types of nests. As with most investigations of habitat quality, the above studies were primarily correlational. They also were based on smaller sample sizes and fewer years of data than the present study. Given the probable subtlety of habitat effects relative to the large between-year and between-individual differences in reproductive success of Magellanic Penguins (Boersma et al. 1990), the large samples and multiple approaches of our study may be essential for detecting biologically important patterns.

METHODS

Study site.—Punta Tombo, Argentina (44°02'S, 65°11'W), the site of the largest mainland colony of Magellanic Penguins (more than 200,000 breeding

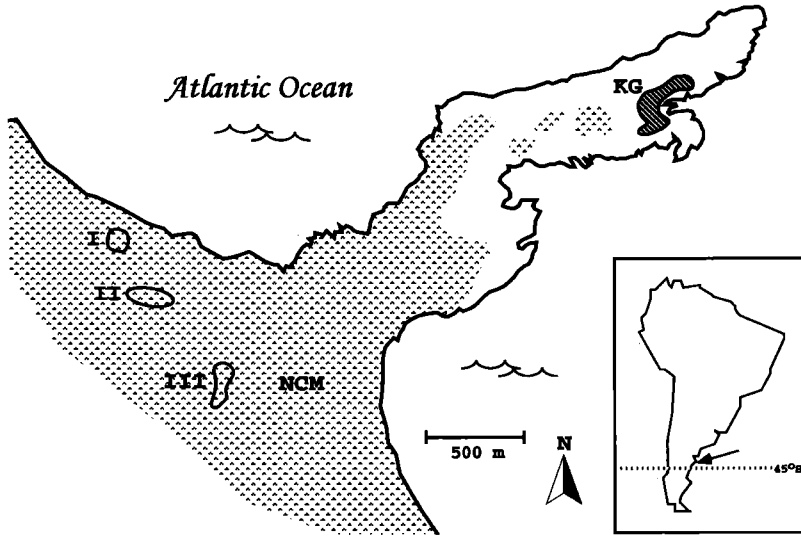


FIG. 1. Punta Tombo, Argentina. Magellanic Penguins nest primarily in shaded area. Study areas (I, II, and III), site of nest-cover manipulation experiment (NCM), and location of Kelp Gull breeding colony (KG) are indicated.

pairs; Boswall and MacIver 1975, Boersma et al. 1990), is near the northern limit of the species' breeding range on the Atlantic coast (Fig. 1). The area is characterized by a cool desert climate. Annual rainfall averages 25 to 30 cm but is highly variable. During the breeding season, daily maximum temperatures can be hot, exceeding 35°C several times in most years. Minimum temperatures rarely drop below 5°C after chicks hatch. Vegetation consists primarily of semidesert scrub dominated by *Lycium* spp. and *Chuquiraga* spp., with lesser amounts of *Suaeda divaricata*, *Schinus polygamus*, *Acacia* spp., *Colliguaya integerrina*, and other species. These bushes generally are 0.75 to 1.5 m tall and 1 to 2 m in diameter, although some *Suaeda* and *Schinus* are twice that height and more than 4 m in diameter. All species except *Lycium*, *Suaeda*, and *Colliguaya* have sharp spines.

Except for small areas without vegetation, most of the colony consists of a mix of burrows and bush nests (Stokes and Boersma 1991). All species of bushes are used for nest sites. A bush nest typically consists of a 40-to-50-cm diameter circular scrape 5 to 20 cm deep (the nest cup) at the base of a bush, covered and surrounded to varying degrees by branches and foliage. An opening (ca. 20 to 40 cm high) on one side of the vegetation is used as an entrance. Bushes vary in foliage density, with some providing scant cover and others completely obscuring the nest cup from view. Burrows range from little more than scrapes with a partial earthen roof to tunnels more than a meter long. A typical burrow has a relatively wide entrance that slopes downhill, narrows to a short neck, and widens into the nest-cup chamber.

On average, burrows provide more cover than bush nests, although the entire range of cover may be found in nests of both types (Table 1).

The Kelp Gull (*Larus dominicanus*) is the main predator of penguin eggs and chicks at Punta Tombo (Yorio and Boersma 1994, pers. obs.). Approximately 5,000 pairs of Kelp Gulls nest in a colony less than 3 km from most of the penguin nests at the colony, including those in our study areas (Fig. 1). Other common predators of penguin eggs and chicks include Patagonian gray foxes (*Dusicyon griseus*), armadillos (*Chaetophractus villosus*), skunks (*Conepatus humboldti*), ferrets (*Lyncodon magellanicus*), and Southern Skuas (*Catharacta antarctica*; Yorio and Boersma 1994).

Data sets.—We used data collected during the 1984 to 1991 breeding seasons in three study areas at Punta Tombo (see Boersma et al. 1990). The study areas, designated Areas I, II, and III, are located at 100, 300, and 600 m inland (approximate median distance), respectively (Fig. 1). Vegetation and nest-type composition in these areas are typical of most of the colony; one-quarter to one-third of the nests are in burrows and the remainder are on the ground beneath bushes. Active nests were permanently marked at the beginning of the study and checked throughout each breeding season to identify breeding pairs and to determine nest attendance, status of nest contents, and fledging success. Every year, all newly active nest sites in the areas were marked and checked. Nests in Areas I and III were checked every 2 to 10 days each season, and those in Area II were checked daily. Breeding birds were marked for identification with numbered stainless steel flipper bands. Chicks were

weighed every 10 days in all areas. We considered a chick to have fledged if it was alive when last seen after 10 January (the approximate date at which chicks begin to fledge) and if it had a mass of at least 1.8 kg the last time it was weighed.

Weather data, including daily maximum, minimum, and current temperature (all $\pm 1^\circ\text{C}$), and daily precipitation, were recorded at approximately 0800 local time at the same shaded location 400 m inland in all years. In 1991, daily maxima and minima also were recorded in Areas I and III.

Each year, study nests were classified by type (burrow, bush, or open scrape) and amount of cover afforded the nest cup: "high" cover nests, with at least 80% of the nest cup obscured from view; "medium," 60 to 79% cover; and "low," less than 60% cover. At least one of us was present every season to standardize data collection by observers. Nests not categorized in a given year were assigned the value of the previous and subsequent year if those values were the same. If those values differed, the unclassified nests were excluded from analyses.

In 1990, we made detailed descriptions of approximately 100 nests in each study area, measuring the height (HEIGHT) and width (WIDTH) of the entrance and the distance from the outside edge of the entrance to the back of the nest cup (LENGTH), as well as estimating to the nearest 5% the amount of cover provided by the nest sides in each of the four compass directions (NORTH, SOUTH, EAST, and WEST) and the roof (ROOF). We standardized estimates of side cover by kneeling to a height of 1 m on the four sides of the nest and estimating the percentage of the nest cup visible from a distance of 1 m. Roof cover similarly was estimated from a position directly above the nest. We measured orientation of the nest entrance to the nearest degree with a compass. Nest type (TYPE; bush or burrow), study area (AREA), and species of bush under which bush nests were located also were recorded.

Experiments.—In addition to gathering descriptive data, we performed two experiments. On 4 November 1990, we designated as a control each medium-cover (60 to 79%) bush nest containing an adult incubating two eggs that we encountered along a transect (NCM in Fig. 1). For each control nest, we then located the two closest medium-cover bush nests with an adult and two eggs, and by coin toss we assigned these two nests to different treatment groups. We clipped some of the branches from the roof and sides of one treatment nest (giving it the cover of a typical low-cover bush nest), and added these branches to the roof and sides of the other (making it a typical high-cover bush nest). We shook the branches of the control nests to mimic the disturbance we caused at the treatment nests. We made 20 replicates, although in one case two of the three birds abandoned their nests during the manipulation. We excluded this set of nests from the analysis, for a to-

tal sample of 19 sets of three nests. To determine survival of nest contents, we marked the eggs and chicks and checked all nests at intervals of 2 to 10 days until 19 December, when chicks were beginning to move from their nests. The 45-day period of the experiment comprised approximately the last third of the 40-day incubation period and the entire early chick-rearing period (to about 30 days after hatching).

To experimentally investigate the effects of nest cover on detection of eggs by predators, we placed chicken eggs in empty penguin nests during the incubation period and monitored disappearance rates. We used three nests of the same type (one of each cover class: high, medium, low) at each of 27 locations spaced at approximately 33-m intervals along transects across the colony. We repeated the procedure using different nests one week later, for a total of 54 sets of three nests (162 nests). The eggs were similar in color to Magellanic Penguin eggs (white) and had a mass of 55 to 65 g, approximately half that of an average Magellanic Penguin egg. We checked all nests every 24 h and noted whether the egg was present. Although placed in empty nests, several chicken eggs were later attended by penguins. Because these eggs probably were not available or visible to predators, any nest in which a penguin was found with an egg was excluded from the analysis.

Analysis.—We compared fledging success of birds in nests that differed in cover and type for each year separately and for all yearly samples pooled. For these comparisons, we restricted our analysis to data from one area (II) to avoid any area-scale differences in success, and because this area was checked most uniformly and frequently over the eight-year period. In this and all other analyses, fledging success was based only on nests where eggs were laid. Because few nests with eggs in Area II were in the low cover category, low- and medium-cover nests were combined.

To control for differences in bird quality, we compared changes in fledging success of pairs that remained together but whose nest-cover class changed between breeding seasons. Cover changed because characteristics of nests changed (72% of 164 pairs of breeding attempts), or because pairs moved (28%). Because birds almost always breed at or near their previous year's nest, possible large-scale location effects on success are controlled for, and all pairs for which reliable fledging success and nest-cover records were available could be included, regardless of study area. To avoid effects of large changes in pair age, a pair's success in a given year was compared with that of the following year if possible (70% of cases), or the year after the following year (30%). All nesting attempts in the 1984 season were excluded from this analysis because in that year nearly all pairs failed to fledge chicks. We tested for differences among groups using a χ^2 test of a 3×2 contingency table. To identify the location of significant differ-

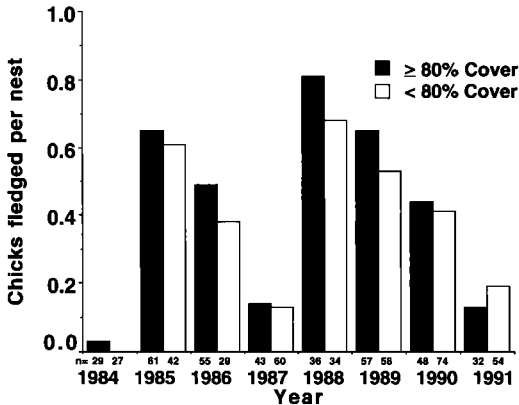


FIG. 2. Magellanic Penguin fledging success by nest cover, 1984 to 1991. Data are from Area II, where nests were checked daily. Yearly mean success of birds using nests with $\geq 80\%$ cover was higher than for birds in nests with less cover (paired $t = 2.45$, $df = 7$, $P < 0.05$).

ences, we partitioned the contingency table following methods in Siegel and Castellan (1988).

To identify the nest characteristics that determine nest quality, we performed a multivariate analysis on the detailed 1990 nest description data. Three dependent binary variables measuring: (1) whether a nest lost at least one egg, (2) whether all chicks of a nest died by age 30 days (when some chicks no longer stay in their home nest), and (3) whether at least one chick from a nest was alive on 10 to 15 January (a measure of fledging success), were analyzed independently by logistic regression (SPSSPC; Norusis 1990) with the following independent variables: NORTH, SOUTH, EAST, WEST, SIDES (the average of the cover on all four sides), ROOF, HEIGHT, WIDTH, LENGTH, TYPE, and AREA. The latter two variables were categorical and were coded as deviation contrasts. We transformed the percentage variables using the arcsine transformation. Variables were entered into the equations in forward stepwise fashion, with order of entry determined by significance and removal by the likelihood-ratio statistic.

Experimental data were drawn from matched sets of experimental nests in a randomized complete block design and analyzed using nonparametric analogues of two-way analysis of variance (Conover 1980). To test for differences in survival of nest contents among treatments in the cover-manipulation experiment, we used the Quade test, a two-way analysis of variance on ranks. Blocks consisted of the 19 sets of the three nearby nests of the three treatments (decreased cover, control, and increased cover), and duration (in days) of survival of nest contents was ranked within each block. Cochran's Q -test for related samples of dichotomous variables was used to test

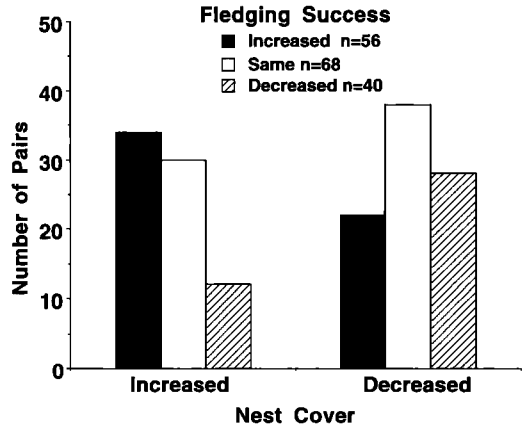


FIG. 3. Change in fledging success (number of chicks fledged) for Magellanic Penguin pairs whose nest cover changed in successive years, 1985 to 1991. More pairs had increased fledging success when their nest cover increased and more had decreased fledging success when their nest cover decreased.

for differences in egg disappearance rates (i.e. presence or absence of eggs) among the three nest-quality classes in the chicken-egg experiment.

RESULTS

Nest cover and fledging success.—Although yearly mean fledging success was extremely variable, over the eight years of the study success was significantly higher at nests with more cover (Fig. 2). On average, birds using nests with low or medium cover fledged 17% fewer chicks per year (0.05 fewer chicks) than those using nests with high cover. The difference was greatest in years of high fledging success, and smallest in years of low success (1984, 1987 and 1991). In two of these low-success years (1984 and 1987), food conditions were poor and nearly all chicks died of starvation. The only year of higher success in nests with less cover was 1991, when 142 mm of rain fell in four days during the early chick-rearing period. This was the most rain to fall in a single storm in any breeding season of the study; it caused extensive flooding of nests, resulting in high chick mortality.

The effect of nest cover on fledging success also was evident in changes in success of pairs whose nest cover changed between years (Fig. 3). Fledging success tended to increase from the previous year when a pair's nest cover increased, and tended to decrease when nest cov-

er decreased ($\chi^2 = 9.31$, $df = 2$, $P < 0.01$). Both increased and decreased fledging success were significantly associated with changes in nest cover (increased vs. same success: $\chi^2 = 5.28$, $df = 1$, $P < 0.01$; decreased vs. same and increased: $\chi^2 = 4.04$, $df = 1$, $P < 0.05$).

Results of the nest-cover manipulation were consistent with the correlative and longitudinal data (Fig. 4). At the end of the experiment, nests with increased cover had more than three times as many surviving chicks (1.58 chicks per nest, $n = 19$) as nests with reduced cover (0.42 chicks per nest, $n = 19$). Survival was intermediate (1.21 chicks per nest, $n = 19$) in control nests (unchanged cover). Differences in ranks of mean number of days a clutch survived (maximum = 45 days) were significant among the three treatments (Quade test, $T = 11.17$, $P < 0.01$), and all treatments differed significantly from each other ($P < 0.05$). Effects of cover during both incubation and chick rearing contributed to the overall pattern; losses of eggs as well as chicks were highest in nests with decreased cover (29% of eggs lost, 70% of chicks), intermediate in control nests (16% of eggs, 25% of chicks), and lowest in nests with added cover (5% of eggs, 17% of chicks).

Elements of cover and other nest variables.—Logistic regression analysis of the 1990 data indicated that amount of roof cover was the only nest-site characteristic significantly related to success or failure of nests, when all variables were considered (Table 2). Univariate results suggested that side cover, especially on the north and west, also was important. However, the measures of side cover were highly correlated with roof cover and were not significant variables in the multivariate solution once roof cover was included. Greater amounts of cover on the roof and north and west sides were significantly associated with lower rates of early chick mortality (Table 3). Height of nest-entrance opening was the most important determinant of egg loss, with eggs in nests with higher entrances at greater risk (Table 4). None of the characteristics explained much of the variance in fledging success (partial correlation coefficient for roof cover = 0.177; Table 2), indicating that other factors also were important.

Nest type (bush or burrow) was not significantly related to any of the measures of success in the multivariate analysis. Consistent with this, although birds nesting in burrows at in-

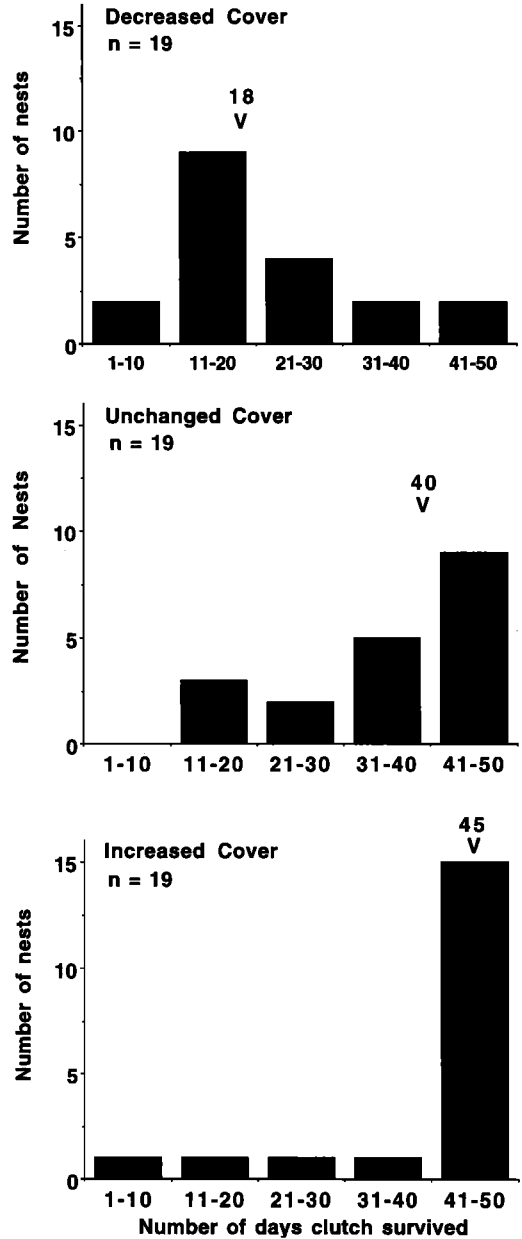


FIG. 4. Survival of nest contents in Magellanic Penguin nests with experimentally manipulated nest cover. Time of survival (days) of eggs and/or chicks in 19 sets of three nests with experimentally decreased (low), increased (high), and unchanged (medium or control) cover over a 45-day period. "V" indicates median number of days of clutch survival for each treatment.

TABLE 2. Magellanic Penguin nest characteristics and fledging success, 1990. Nests in which at least one chick survived through mid-January (successful) are compared with nests in which no chicks survived (unsuccessful). Logistic regression values are estimates of significant parameters; *P*- and *R*-values are based on all significant variables entered in the equation.

Variable	ANOVA ^a			Logistic regression		
	Unsuccessful	Successful	<i>F</i>	Estimate	<i>P</i>	<i>R</i>
NORTH	67.2 ± 2.93	77.2 ± 2.94	5.68*		0.055	0.064
EAST	67.9 ± 3.03	64.0 ± 3.56	0.70		0.124	0.030
SOUTH	65.8 ± 3.04	68.4 ± 3.32	0.36		0.955	0.000
WEST	68.4 ± 3.01	77.0 ± 2.93	4.18*		0.108	0.038
ROOF	79.7 ± 1.56	87.6 ± 1.34	14.20***	0.029***	0.000	0.177
SIDES	67.4 ± 0.92	71.8 ± 0.81	12.47***		0.164	0.055
HEIGHT	27.5 ± 1.01	25.7 ± 0.68	1.96		0.975	0.000
WIDTH	41.8 ± 0.87	41.8 ± 0.80	0.00		0.646	0.000
LENGTH	77.3 ± 2.32	79.5 ± 2.26	0.46		0.433	0.000
TYPE ^b					0.137	0.000
AREA ^b					0.551	0.000

*, *P* < 0.05; **, *P* < 0.01; ***, *P* < 0.001.
^a Values are $\bar{x} \pm SE$; *n* = 158 unsuccessful nests, 138 successful nests.
^b Categorical variables.

land study areas in 1990 were more likely to fledge chicks than were birds nesting under bushes ($\chi^2 = 4.04$, *df* = 1, *P* < 0.05, *n* = 197), fledging success did not differ significantly between high-cover nests of the two types ($\chi^2 = 1.19$, *df* = 1, *P* < 0.30, *n* = 113). Similarly, in the eight yearly samples from Area II, average fledging success at burrow nests (\bar{x} = 0.43) was higher, although not significantly so, than that at bush nests (\bar{x} = 0.38; paired *t* = 1.54, *df* = 7, *P* < 0.20). Considering only nests with high cover, success of the two nest types was about the same (\bar{x} = 0.43 vs. 0.42, respectively; *t* =

0.62, *df* = 7, *P* < 0.50). Thus, any advantage in fledging success of burrows versus bush nests (if one exists at all) appears to be a function of the greater cover provided by burrow nests.

The type of bush under which nests were located also had no effect on success. In the two inland study areas (where species composition of bushes was similar), pairs nesting under *Chuquiraga* (spiny) and *Lycium* (not spiny) bushes had similar fledging success ($\chi^2 = 0.001$, *df* = 1, *P* = 0.98, *n* = 153). The probability of egg loss also was unrelated to whether bushes had spines ($\chi^2 < 0.001$, *df* = 1, *P* = 1.0,

TABLE 3. Magellanic Penguin nest characteristics and chick survival to 30 days. Nests in which at least one chick survived the early chick-rearing period (successful) are compared with nests in which neither chick survived (unsuccessful). Logistic regression values are estimates of significant parameters; *P*- and *R*-values are based on all significant variables entered in the equation.

Variable	ANOVA ^a			Logistic regression		
	Unsuccessful	Successful	<i>F</i>	Estimate	<i>P</i>	<i>R</i>
NORTH	65.4 ± 3.63	76.6 ± 2.87	6.00*	0.011*	0.016	0.104
EAST	68.9 ± 3.74	65.4 ± 3.41	0.47		0.602	0.000
SOUTH	70.0 ± 3.47	67.4 ± 3.25	0.28		0.653	0.000
WEST	66.3 ± 3.77	76.4 ± 2.88	4.71*	0.010*	0.033	0.086
ROOF	80.8 ± 1.79	87.8 ± 1.28	10.87**	0.020*	0.023	0.095
SIDES	67.7 ± 1.11	71.6 ± 0.80	8.45**		0.651	0.000
HEIGHT	25.6 ± 0.72	25.5 ± 0.64	0.01		0.393	0.000
WIDTH	41.8 ± 0.86	41.6 ± 0.76	0.04		0.647	0.000
LENGTH	75.4 ± 2.48	78.4 ± 2.14	0.82		0.204	0.000
TYPE ^b					0.902	0.000
AREA ^b					0.632	0.000

*, *P* < 0.05; **, *P* < 0.01; ***, *P* < 0.001.
^a Values are $\bar{x} \pm SE$; *n* = 108 unsuccessful nests, 148 successful nests.
^b Categorical variables.

TABLE 4. Magellanic Penguin nest characteristics and egg loss. Nests in which at least one egg was lost are compared with nests that did not lose eggs. Logistic regression values are estimates of significant parameters; *P*- and *R*-values are based on all significant variables entered in the equation.

Variable	ANOVA ^a			Logistic regression		
	Eggs lost	Eggs not lost	<i>F</i>	Estimate	<i>P</i>	<i>R</i>
NORTH	71.3 ± 4.27	72.1 ± 2.39	0.03		0.918	0.000
EAST	60.7 ± 4.83	68.1 ± 2.60	1.81		0.206	0.000
SOUTH	65.7 ± 4.74	67.2 ± 2.54	0.08		0.678	0.000
WEST	72.9 ± 4.27	72.6 ± 2.41	0.00		0.701	0.000
ROOF	79.2 ± 2.56	84.8 ± 1.13	5.04*		0.148	0.017
SIDES	67.8 ± 1.53	70.1 ± 0.67	2.45		0.192	0.000
HEIGHT	29.9 ± 2.13	25.6 ± 0.50	8.55***	0.038***	0.004	0.143
WIDTH	43.0 ± 1.65	41.4 ± 0.59	1.31		0.365	0.000
LENGTH	80.6 ± 4.04	77.6 ± 1.74	0.56		0.304	0.000
TYPE ^b					0.258	0.000
AREA ^b				*	0.026	0.102
AREA(I)				0.313	0.122	0.035
AREA(II)				0.274	0.166	0.000

*, *P* < 0.05; **, *P* < 0.01; ***, *P* < 0.001.

^a Values are $\bar{x} \pm SE$; *n* = 67 nests with eggs lost, 233 nests with no eggs lost.

^b Categorical variables.

n = 153). Nests under the two types of bushes did not differ significantly in any of the measured nest characteristics except length (i.e. distance from mouth of entrance to back of nest chamber; \bar{x} = 69.0 vs. 87.1, *t* = 2.60, *df* = 361, *P* < 0.01), probably a result of the smaller average size of *Chuquiraga* bushes.

Nest orientation, grouped in categories of 45° (N, NE, E, etc.), was not significantly related to fledging success (χ^2 = 7.51, *df* = 7, *P* < 0.40, *n* = 296). However, when categories were lumped, differentiating only between nests with entrances facing north versus south of an east-west plane, success was lower in nests facing north (χ^2 = 3.90, *df* = 1, *P* < 0.05, *n* = 296). The relationship was significant among burrows (χ^2 = 4.87, *df* = 1, *P* < 0.05, *n* = 106) but not bush nests (χ^2 = 0.47, *df* = 1, *P* < 0.50, *n* = 190).

Nest characteristics and temperature.—Area I is 100 m from the mean high tide line and often is slightly cooler than sites farther inland. For example, during the 1991 breeding season, the average daily maximum temperature in Area I was 1.6°C lower (SD = 3.0) than in Area III, and the maximum temperature for the period was 2°C lower. When the multivariate analysis of 1990 data shown in Table 2 was repeated for inland sites only (Area I nests excluded), nest cover on the north side (as well as roof cover) was a significant variable (*R* = 0.103, *P* < 0.05, *n* = 218) in the logistic regression for fledging success, suggesting a sun-protection function

of nest cover and greater importance of such protection at inland sites. This is illustrated by univariate comparisons of nests in Areas I and III: roof cover was significantly associated with success in both areas, but north-side cover was associated with success only at inland sites (Fig. 5).

In hot, sunny weather, daily maximum temperatures are higher in nests with less cover. For example, on a day with midday shade temperatures typical of the early chick-rearing period (25 to 30°C), the temperature in a bush nest with low cover exceeded 40°C, more than 10°C hotter than in a bush nest with high cover. On hot days, chicks in exposed nests often move to more shaded locations, usually other nests that are not currently occupied by adults (pers. obs.). In 1990, nests from which chicks moved (*n* = 30) averaged 10% less roof cover than nests of chicks that did not move (*n* = 107; *t* = 3.15, *df* = 135, *P* < 0.01). Of chicks that moved, twice as many moved to nests with more cover (*n* = 18) than to nests with less cover (*n* = 9; three moved to locations of unknown or equal cover). Less cover also was associated with movement of chicks at younger ages. Among nests of chicks that survived until mid-January, roof cover averaged 63.0% (*n* = 7) for nests with chicks that first moved at 30 days or younger (i.e. the age at which chicks begin to be left unattended) and averaged 81.4% (*n* = 31) in nests where chicks first moved when they were older than 30 days (*t* = 2.48, *P* < 0.05). The nest-

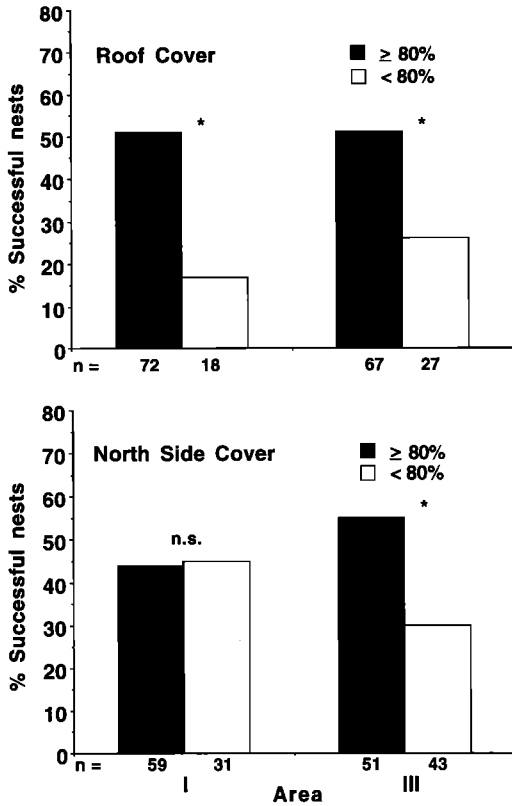


FIG. 5. Effect of roof cover (upper) and north-side cover (lower) on fledging success at Magellanic Penguin nests in seaside (Area I) and inland (Area III) study areas, 1990. Roof cover was significantly related to success in both areas (Area I: $\chi^2 = 5.70$, $df = 1$, $P < 0.05$, $n = 90$; Area III: $\chi^2 = 3.86$, $df = 1$, $P < 0.05$, $n = 94$). North-side cover was related to success only in inland area (Area I: $\chi^2 = 0.01$, $df = 1$, $P < 1.0$, $n = 90$; Area III: $\chi^2 = 4.81$, $df = 1$, $P < 0.05$, $n = 94$). Asterisks indicate significant difference at $P < 0.05$.

cover manipulation experiment also showed the influence of nest cover on chick movement. By the end of the experiment, chicks from nests with decreased cover were more likely to have moved (63% moved, $n = 8$) than chicks from control (14%, $n = 22$) or improved (3%, $n = 29$) nests ($G = 11.95$, $df = 2$, $P < 0.01$).

We observed no large-scale die-offs during hot spells (cf. Salzman 1982). However, daily chick mortality rates in 1990 were significantly higher on the hottest days in late November, when most chicks were younger than 20 days old. In a sample of chicks monitored daily ($n = 206$), 5.3% died on a day of high maximum temperature (38°C) versus an average of 2.1% in the

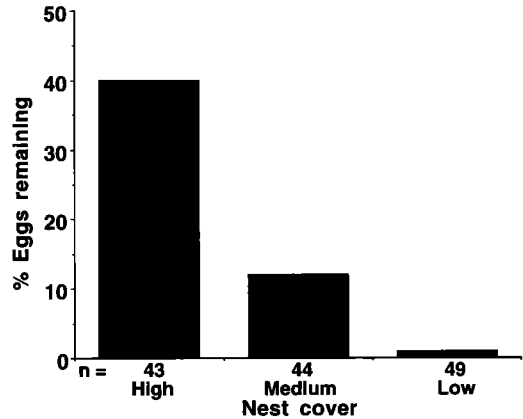


FIG. 6. Percent of chicken eggs remaining in unoccupied Magellanic Penguin nests with high, medium, and low cover after 24 h, November 1990. Nests occupied by penguins before eggs disappeared were excluded ($n = 26$). The difference among treatments was highly significant ($\chi^2 = 24.2$, $df = 2$, $P < 0.001$, $n = 136$).

two preceding and following days (\bar{x} maximum = 24°C; $\chi^2 = 5.01$, $df = 1$, $P < 0.05$, $n = 980$ mortality chances). Roof cover of nests where chicks died on the two days in late November when ambient temperatures exceeded 30°C was lower (70.8%, $n = 24$) than at nests where chicks died on the preceding and following cooler days (81.4%, $n = 51$; $t = 2.74$, $P < 0.01$).

Nest characteristics and predation.—Consistent with the multivariate results for egg loss (Table 4), in the sample of all nests in 1990, egg-predation rates were lower in nests with entrance heights less than 30 cm than in those with taller entrances ($\chi^2 = 3.82$, $df = 1$, $P < 0.10$, $n = 300$). Univariate results also suggested a possible effect of roof cover on egg loss (Table 4), and more egg loss occurred in nests with less than 80% roof cover than in those with more roof cover ($\chi^2 = 4.36$, $df = 1$, $P < 0.05$, $n = 300$). Entrance height and roof cover were moderately negatively correlated ($R = -0.43$).

The chicken-egg predation experiment indicated a strong influence of nest cover on the rate of egg detection by predators, with eggs more likely to remain undisturbed in nest sites with more cover (Fig. 6). In the 28 sets of three nests in which none of the nests was occupied by a penguin (i.e. a randomized complete block design), treatment differences were highly significant, and the likelihood of retaining an egg over successive 24-h periods was positively

correlated with greater cover (Cochran's $Q = 25.75$, $P < 0.001$). This sample included both bush nests and burrows; the positive effect of cover also was evident ($P < 0.01$) for each nest type considered separately.

Nearly all (93%, $n = 150$) of the chicken eggs (including those found attended) were depredated after three days. Of the 12 eggs that remained, all except one were in high-cover nests. Five of the 12, including the one in a medium-cover nest, had been attended by penguins during at least one nest check and may have been inaccessible to most predators.

Our daily observations of adult nest attendance suggest a link between thermal properties of nests and predation. Eggs that were depredated often had been previously left unattended. Of the 71 nests in Area II known to have been unattended on at least one day during the incubation stage, 32% suffered predation compared with only 13% of nests not known to have been unattended ($n = 805$; $\chi^2 = 25.4$, $df = 1$, $P < 0.001$). Neglect of nest contents was more likely to occur on hot days, when adults sometimes left the nest and stood panting in nearby shade, and occasionally left the area (pers. obs.). Among Area II nests from 1984 to 1991, maximum temperatures were significantly higher on the first day nests were unattended than on the previous day (paired $t = 2.05$, $df = 57$, $P < 0.05$) during incubation and early chick rearing in warm weather (T_{max} on both days $> 20^\circ\text{C}$). Among nests with detailed nest descriptions in 1990, those that were unattended for at least one day had less roof cover ($\bar{x} = 74.1\%$) than those not known to have been unattended ($\bar{x} = 83.7\%$; $t = 2.37$, $df = 314$, $P < 0.05$).

DISCUSSION

Nest characteristics and reproductive success.—Cross-sectional, longitudinal, and experimental data demonstrate that amount of nest cover is a significant determinant of reproductive success in Magellanic Penguins, with greater amounts of cover producing higher fledging success. The magnitude of the effect of cover is small in a single season, especially compared with the large between-year differences in colony-wide fledging success (Fig. 2). However, the benefits of cover are present in nearly all years and are likely to have a significant effect

on fitness over the lifetime of a penguin. Because Magellanic Penguins are highly site faithful (Stokes 1994), individuals are likely to nest under similar cover conditions—often using the same nest—for much or all of their reproductive lives. Based on band resightings and data on fledging success from 1983 to 1992 (Boersma unpubl. data), we estimate that the average adult penguin at Punta Tombo probably breeds for approximately eight seasons and fledges fewer than four chicks. Thus, nesting at a high-cover site, which confers an average yearly advantage of an additional 0.05 chicks fledged, could increase a pair's expected lifetime reproductive success by 0.4 chicks, or more than 10% of expected lifetime output.

The importance and variability of other influences on fledging success (e.g. food conditions, parental quality, weather) probably explain why, in the logistic regression analysis, nest characteristics accounted for only a small amount of the variance. Food availability probably is the most important of these other factors (Boersma et al. 1990, Boersma and Stokes 1995). The effect of nest cover on success is less pronounced in years of low fledging success, presumably because in those years survival of chicks depends primarily on the ability of parents to forage effectively under conditions of poor food availability. High annual variability in fledging success due to food conditions also explains the exceptions to the general pattern in the longitudinal results (i.e. pairs that increased their nest cover but had reduced success and vice versa).

The contrary pattern observed in 1991, when fledging success was higher for birds in nests with less cover, was due to exceptionally heavy rains and flooding of nests when chicks were very young. Flooding of a nest before eggs hatch and chicks are old enough to move to high ground usually results in loss of the nest contents. In 1991, flooding occurred in nests of all amounts of cover, but because deep burrows with wide openings can collect large amounts of water during rainstorms (Stokes and Boersma 1991), some of the nests with the most cover experienced the worst flooding. Thus, the advantages of good cover provided by some burrows were offset by greater susceptibility to flooding. Flooding severe enough to have this effect appears to be infrequent. No event comparable to the 1991 storm occurred at Punta

Tombo from 1982 to 1993; the amount of rain was more than twice the amount that fell during the entire 70-day incubation and early chick-rearing periods of the next wettest season (1985). A local resident whose family has lived at the ranch adjoining the colony since the early 1900s described the storm as very unusual for that time of year.

Although in some cases (e.g. inland sites) fledging success was higher in burrows than bush nests, success in nests of the two types did not differ when only high-cover nests were considered, indicating no advantage to burrows per se. Similarly, spininess of the bush under which a nest was located did not affect fledging success. These results indicate that it is the amount of cover, rather than the type, that is important in determining success.

The longitudinal and experimental results confirm the importance of cover for fledging success. That the same breeding pairs had higher and lower success in years when they used nests with more and less cover, respectively, suggests that nest quality itself, rather than bird quality, confers the observed reproductive advantage. This result leaves open the possibility that pairs vary by season in some quality (e.g. body condition) that affects fledging success and coincidentally affects ability to acquire a high-quality nest (Ens et al. 1992). However, the nest-cover manipulation experiment shows that cover is an important determinant of success regardless of yearly differences in pair condition. Even if body condition and nest cover are positively correlated, the initial similarity of the experimental nests would indicate that all occupants were of approximately equal condition. Each increment of cover increase (low to medium and medium to high) produced a significant increase in success. The difference was greatest between low and medium cover (control) nests, which is consistent with the conclusion that having more than minimal cover is the main significance of nest cover for success (see de Bary 1990, Gandini 1993). However, the difference in success between medium- and high-cover nests demonstrates a significant advantage of additional cover beyond a moderate amount.

An interesting aspect of our results is the contrast between the decisive effect of nest cover on success demonstrated by the experimental cover manipulation versus the smaller effect

found in the cross-sectional data. One would expect a similar level of effect in the two samples, or, if nest quality and bird quality were positively correlated, the apparent effect of nest cover on success should be more pronounced in the correlative results. One interpretation of this unexpected result is that poor sites offer advantages to fledging success that partly offset the drawbacks of poor cover. Possible advantages include less competition for nest sites and familiarity with sites and neighbors. For example, intraspecific aggression occurs more frequently at better nests (Stokes 1994) and appears to have a significant effect on survival of nest contents (Yorio and Boersma 1994). Birds in poor sites may avoid some of these costs.

Adult behaviors also may be matched to, and partly compensate for, the characteristics of the nest. For example, birds that occupy nests with less cover may spend more time shading eggs and chicks than do birds in better nests. A mechanism for this matching could be the pattern of breeding-site fidelity that occurs in this species (Stokes 1994). Although breeders generally are site faithful, re-use of the previous year's nest site is partly contingent on previous fledging success. Thus, birds that exhibit appropriate behaviors for the cover conditions of their nests will tend to succeed in fledging chicks and return to those nests; those that do not succeed will be more likely to move to new sites, where their behaviors may be more appropriate. Such compensating behaviors could carry energetic, mortality, or long-term reproductive costs that are not reflected in a single season's reproductive success.

Temperature.—Our results suggest that protection from sun is an important function of nest cover. Overhead cover was the only variable in the multivariate analysis that contributed significantly to fledging success. Univariate tests indicated that cover on north and west sides (the sides predicted to be most critical for shade) also may be important, and cover on the north and west sides was a significant determinant of chick survival. The significant effect on fledging success of north-side cover at warmer sites and higher success of birds in nests with entrances oriented away from north also support this conclusion.

These results are not due to unusually warm weather in 1990. The mean daily maximum

shade temperature from 15 November to 15 December (when nest contents are most vulnerable to high temperatures) in 1990 was 25.9°C, the nine-year (1983 to 1991) median for that period. The 1990 season was fourth out of nine years in the number of days with maximum temperatures exceeding 30°C (6 days; range 3 in 1985 and 1986, 19 in 1983).

The absence of a significant effect of nest orientation at a finer scale (by 45° categories) may be due to variability of side cover: many nests are highly exposed to sun from sides other than the entrance. This is particularly true of bush nests and probably explains why orientation is associated with success in burrows (which usually are exposed only on the entrance side) but not in bush nests. Bush nests also are more likely to be located near (and shaded by) other bushes, which would further obscure the effect of orientation. Moreover, burrows may have thermal properties that make orientation a more critical component of nest design. For example, late-afternoon sun shining into an unoccupied burrow elevated the inside temperature to 50°C, or 23°C higher than ambient; temperatures in a nearby bush nest at the same time were only 2°C above ambient (Stokes unpubl. data). The elevated temperature in burrows receiving direct sun presumably is due to re-radiation from exposed inside surfaces; such re-radiation has been proposed as a determinant of breeding-site suitability in other seabirds (Burger and Gochfeld 1991).

The significance of roof, north-, and west-side cover in explaining mortality of young chicks, and the higher mortality of young chicks on hot days in nests with less cover, suggests that the primary thermal importance of nest cover is protection of young chicks from high temperatures. Most of the mortality of Magellanic Penguin chicks occurs when chicks are less than 20 days old (Boersma and Stokes 1995) and probably are unable to thermoregulate effectively. Erasmus and Smith (1974) found that Jackass Penguin chicks could not thermoregulate in cold temperatures before they grew to at least 400 g, a mass typically attained by Magellanic Penguins at 10 to 20 days of age.

Predation.—Protection of nest contents from predation is another benefit of nest cover suggested by both the multivariate analysis and the experimental results. In most of the colony,

Kelp Gulls appear to locate vulnerable eggs and chicks from the air (Yorio and Boersma 1994). The results of the chicken-egg experiment suggest that eggs and chicks in nests with more overhead cover are less likely to be detected by gulls.

Once a predator, gull or mammal, detects an egg or chick, it must be able to reach the nest cup. Typically, the size of the largest opening in the side cover (usually the entrance) will determine whether the predator can enter. Indeed, nest-entrance height may be the most critical characteristic of a nest during incubation (Table 4), when high temperatures are less frequent than during the chick-rearing period and predation is a greater threat than heat stress. Although entrance height ($\bar{x} = 27$ cm, $n = 196$) probably is not a constraint for small predators (e.g. armadillos, ferrets, and skunks), at least two major predators, Kelp Gulls and foxes, are likely to be constrained by entrance height. A high entrance also may increase detection of eggs from the air by increasing the angle from which the nest cup can be seen.

Protection from predation and heat stress are not entirely distinct functions of nest cover (Jehl and Mahoney 1987). An adult penguin in a nest presents a formidable defense to most predators. Although some predators (armadillos and gulls) can take eggs and chicks while adults are present, predation is more likely to occur when nests are unattended (Yorio and Boersma 1994). This is indicated by the high disappearance rate of eggs from empty nests in the chicken-egg experiment. Our results suggest that birds in nests with less cover are more likely to temporarily leave the nest because of heat stress, and consequently to expose their eggs or chicks to risk of predation. This is consistent with studies of other *Spheniscus* species, which found that heat stress caused nest desertion (e.g. Boersma 1976, LaCock 1988).

In addition, a chick that moves because of high temperatures in a poorly covered nest may face increased risk of predation while moving, as well as a host of other indirect costs. The chick may be more likely to miss feedings than chicks that stay at home, because parents usually return to the nest to feed chicks. Even if the chick returns to the natal nest for feedings, it may receive less food because some may be digested by the waiting parent before the chick arrives. Finally, by leaving its home

nest, a chick may increase its risk of being injured or killed by other adults.

Nest quality and nest use.—Despite the clear advantage of greater amounts of nest cover for fledging success, penguins nonetheless use sites of widely differing cover and often continue to use poor sites when better sites exist nearby. This reflects the constraints—physical, social, and informational—to which penguins are subject when choosing nest sites (Stokes 1994). The number of high-cover nests at Punta Tombo is limited, and birds must compete for them. The benefits of a high-cover site may be outweighed by the costs of acquiring it. Moreover, considerations besides the amount of cover may affect the relative value of nests. For instance, small numbers of incubating adults are killed in their burrows when occasional heavy rain saturates the ground, causing burrows to collapse (Stokes and Boersma 1991). Although slight (estimated risk of death by burrow collapse <0.2% per year), this mortality factor is not faced by birds in bush nests. In addition, although generally stable, some nests of both types deteriorate over time. Over the course of several years, some bushes provide less shelter as twigs are broken off for nesting material, roots are killed during nest-cup excavation, or soil becomes unfavorable for plant growth due to high concentrations of guano (Pisano 1971). If bush cover declines, a bird must dig a burrow under the bush, move, or remain in a nest of reduced quality. Burrows sometimes must be re-excavated depending on the amount of deterioration that occurs during winter. This can require substantial movement of substrate (ca. 5×10^4 cm³ for a complete burrow [Stokes and Boersma 1991]), which doubtless is energetically costly. Thus, although the value of a nest primarily is a result of the cover it provides, acquisition costs, mortality factors, and long-term maintenance costs may modify that value.

CONCLUSIONS

By reducing exposure of nest contents to predators and high temperatures, greater amounts of nest cover have a positive effect on fledging success of Magellanic Penguins. Longitudinal and experimental data confirm that the reproductive advantage of sites with more cover results from the quality of the sites themselves and not simply the quality of the birds

in those sites. The effect of nest cover on fledging success is small relative to annual variability in success due to food conditions, but because penguins reproduce for many seasons and are site faithful, the yearly effect of nest cover is likely to influence lifetime reproductive success substantially. Thus, fitness of Magellanic Penguins appears to be significantly affected by habitat characteristics at the nest-site scale. With increasing alteration of coastal environments by humans, protection of this species, as well as other *Spheniscus* species and burrowing seabirds in general, requires the identification and preservation of breeding habitats that include the elements necessary for successful reproduction. In particular, these habitats must provide sites with cover that allows nesting birds to avoid high temperatures and predation.

Unlike other studies of Magellanic Penguins that were limited to fewer years, smaller sample sizes, and mostly correlative approaches, our study found significant effects of relatively small differences in nest cover. This shows the importance of large and long-term data sets and experimental approaches in identifying subtle but biologically meaningful factors. Such tools are likely to be important in the study and conservation of any long-lived organism inhabiting a variable environment.

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LITERATURE CITED

- AUSTIN, G. T. 1976. Behavioral adaptations of the Verdin to the desert. *Auk* 93:245–262.
- BERGIN, T. M. 1992. Habitat selection by the Western Kingbird in western Nebraska: A hierarchical analysis. *Condor* 94:903–911.
- BEST, L. B., AND D. F. STAUFFER. 1980. Factors affecting nesting success in riparian bird communities. *Condor* 82:149–158.

- BIRKHEAD, T. R., E. GREENE, J. D. BIGGINS, AND D. N. NETTLESHIP. 1985. Breeding site characteristics and breeding success in Thick-billed Murres. *Canadian Journal of Zoology* 63:1880-1884.
- BOERSMA, P. D. 1975. Adaptation of Galapagos Penguins for life in two different environments. Pages 101-114 in *The biology of penguins* (B. Stonehouse, Ed.). Macmillan, London.
- BOERSMA, P. D. 1976. An ecological and behavioral study of the Galapagos Penguin. *Living Bird* 15: 43-93.
- BOERSMA, P. D., AND D. L. STOKES. 1995. Mortality patterns, hatching asynchrony, and size asymmetry in Magellanic Penguin (*Spheniscus magellanicus*) chicks. Pages 3-25 in *Penguin biology* (P. Dann, I. Norman, and P. Reilly, Eds.). Surrey Beatty, Sydney, Australia.
- BOERSMA, P. D., D. L. STOKES, AND P. M. YORIO. 1990. Reproductive variability and historical change of Magellanic Penguins (*Spheniscus magellanicus*) at Punta Tombo, Argentina. Pages 13-43 in *Penguin biology* (L. Davis and J. Darby, Eds.). Academic Press, San Diego.
- BOSWALL, J., AND D. MACIVER. 1975. The Magellanic Penguin *Spheniscus magellanicus*. Pages 271-305 in *The biology of penguins* (B. Stonehouse, Ed.). Macmillan, London.
- BURGER, J., AND M. GOCHFELD. 1991. Nest-site selection by the Herald Petrel and White-tailed Tropicbird on Round Island, Indian Ocean. *Wilson Bulletin* 103:126-130.
- CONOVER, W. S. 1980. *Practical non-parametric statistics*, 2nd ed. John Wiley and Sons, New York.
- COULSON, J. C. 1968. Differences in the quality of birds nesting in the centre and on the edges of a colony. *Nature* 217:478-479.
- DE BARY PEREDA, S. 1990. Influence of nest-site characteristics on the reproductive success of Magellanic Penguins. M.S. thesis, University of Washington, Seattle.
- DOBKIN, D. S. 1985. Heterogeneity of tropical floral microclimates and the response of hummingbird flower mites. *Ecology* 66:536-543.
- ENS, B. J., M. KERSTEN, A. BRENNINKMEIJER, AND J. B. HULSCHER. 1992. Territory quality, parental effort and reproductive success of Oystercatchers (*Haematopus ostralegus*). *Journal of Animal Ecology* 61:703-715.
- ERASMUS, T., AND D. SMITH. 1974. Temperature regulation of young Jackass Penguins *Spheniscus demersus*. *South African Journal of Zoology* 9:195-203.
- FINCH, D. M. 1989. Relationships of surrounding riparian habitat to nest-box use and reproductive outcome in House Wrens. *Condor* 91:848-859.
- FRERE, E., P. GANDINI, AND P. D. BOERSMA. 1992. Effects of nest type and location on reproductive success of the Magellanic Penguin *Spheniscus magellanicus*. *Marine Ornithology* 20:1-6.
- FROST, P. G. H., W. R. SIEGFRIED, AND A. E. BURGER. 1976a. Behavioral adaptations of the Jackass Penguin *Spheniscus demersus* to a hot, arid environment. *Journal of Ecology* 179:165-187.
- FROST, P. G. H., W. R. SIEGFRIED, AND J. COOPER. 1976b. The conservation of the Jackass Penguin. *Biological Conservation* 9:79-99.
- GANDINI, P. A. 1993. Patron de nidification en el pingüino de Magallanes. Ph.D. dissertation, Universidad de Buenos Aires, Buenos Aires.
- HATCHWELL, B. J., D. E. CHAMBERLAIN, AND C. M. PERRINS. 1996. The reproductive success of Blackbirds *Turdus merula* in relation to habitat structure and choice of nest site. *Ibis* 118:256-262.
- HOLWAY, D. A. 1991. Nest-site selection and the importance of nest concealment in the Black-throated Blue Warbler. *Condor* 93:575-581.
- HOWLETT, J. S., AND B. J. STUTCHBURY. 1996. Nest concealment and predation in Hooded Warblers: Experimental removal of nest cover. *Auk* 113:1-9.
- HUDSON, P. J. 1982. Nest site characteristics and breeding success in the Razorbill *Alca torda*. *Ibis* 124:355-359.
- JACKSON, S. L., D. S. HIK, AND R. F. ROCKWELL. 1988. The influence of nesting habitat on reproductive success of the Lesser Snow Goose. *Canadian Journal of Zoology* 66:1699-1703.
- JEHL, J. R., AND S. A. MAHONEY. 1987. The roles of thermal environment and predation in habitat choice in the California Gull. *Condor* 89:850-862.
- KEPPIE, D. M., AND P. W. HERZOG. 1978. Nest-site characteristics and nest success of Spruce Grouse. *Journal of Wildlife Management* 42:628-632.
- LACOCK, G. D. 1988. Effect of substrate and ambient temperature on burrowing African Penguins. *Wilson Bulletin* 100:132-134.
- LEVINS, R. 1968. *Evolution in changing environments*. Princeton University Press, Princeton, New Jersey.
- MARTIN, T. E., AND J. J. ROPER. 1988. Nest predation and nest-site selection of a western population of the Hermit Thrush. *Condor* 90:51-57.
- MORSE, D. H., AND S. W. KRESS. 1984. The effect of burrow loss on mate choice in the Leach's Storm-Petrel. *Auk* 101:158-160.
- NETTLESHIP, D. N. 1972. Breeding success of the Common Puffin (*Fratercula arctica*) on different habitats at Great Island, Newfoundland. *Ecological Monographs* 42:239-268.
- NORMENT, C. J. 1993. Nest-site characteristics and nest predation in Harris' Sparrows and White-crowned Sparrows in the Northwest Territories, Canada. *Auk* 110:769-777.
- NORUSIS, M. J. 1990. *SPSS advanced statistics*. SPSS Inc., Chicago.
- ORIAN, G. H., AND J. F. WITTENBERGER. 1991. Spa-

- tial and temporal scales in habitat selection. *American Naturalist* 137:S29-S49.
- PISANO, E. 1971. Estudio ecologico preliminar de Parque Nacional 'Los Pinguinos' (Estrecho de Magallanes). *Annals del Instituto Patagonico* 2: 76-95.
- PLEZCZYNSKA, W. K. 1978. Microgeographic prediction of polygyny in the Lark Bunting. *Science* 201:935-937.
- PUGESEK, B. H., AND K. L. DIEM. 1983. A multivariate study of the relationship of parental age to reproductive success in California Gulls. *Ecology* 64:829-839.
- REITSMA, L. R., R. T. HOLMES, AND T. W. SHERRY. 1990. Effects of removal of red squirrels (*Tamiasciurus hudsonicus*) and eastern chipmunks (*Tamias striatus*) on nest predation in northern hardwood forest: An artificial nest experiment. *Oikos* 57:375-380.
- RENDELL, W. B., AND R. J. ROBERTSON. 1989. Nest-site characteristics, reproductive success and cavity availability for Tree Swallows breeding in natural cavities. *Condor* 91:875-885.
- RICKLEFS, R. E., AND F. R. HAINSWORTH. 1969. Temperature regulation in nestling Cactus Wrens: The nest environment. *Condor* 71:32-37.
- RIECHERT, S. E., AND C. R. TRACY. 1975. Thermal balance and prey availability: Bases for a model relating web-site characteristics to spider reproductive success. *Ecology* 56:265-284.
- SALZMAN, A. G. 1982. The selective importance of heat stress in gull nest location. *Ecology* 63:742-751.
- SARGENT, R. C., AND J. B. GEBLER. 1980. Effects of nest site concealment on hatching success, reproductive success, and parental behavior of the threespine stickleback (*Gasterosteus aculeatus*). *Behavioral Ecology and Sociobiology* 7:137-142.
- SIEGEL, S., AND N. J. CASTELLAN, JR. 1988. *Nonparametric statistics for the social sciences*. McGraw-Hill, New York.
- SMITH, C. C. 1968. The adaptive nature of social organization in the genus of tree squirrels *Tamiasciurus*. *Ecological Monographs* 38:31-64.
- STOKES, D. L. 1994. Nesting habitat use, value, and selection in the Magellanic Penguin (*Spheniscus magellanicus*). Ph.D. dissertation, University of Washington, Seattle.
- STOKES, D. L., AND P. D. BOERSMA. 1991. Effects of substrate on the distribution of Magellanic Penguin (*Spheniscus magellanicus*) burrows. *Auk* 108: 922-933.
- STONEHOUSE, B. 1967. The general biology and thermal balance of penguins. *Advances in Ecological Research* 4:131-196.
- STONEHOUSE, B. 1970. Adaptation in polar and sub-polar penguins (*Spheniscidae*). Pages 526-541 in *Antarctic ecology* (M. W. Holdgate, Ed.). Academic Press, London.
- SWINGLAND, I. R. 1983. Interspecific differences in movement. Pages 102-115 in *The ecology of animal movement* (I. R. Swingland and P. J. Greenwood, Eds.). Oxford University Press, Oxford.
- WALSBERG, G. E. 1985. Physiological consequences of microhabitat selection. Pages 389-413 in *Habitat selection in birds* (M. L. Cody, Ed.). Academic Press, New York.
- WIENS, J. A. 1985. Habitat selection in variable environments: Shrub-steppe birds. Pages 227-251 in *Habitat selection in birds* (M. L. Cody, Ed.). Academic Press, New York.
- WIENS, J. 1986. Spatial scale and temporal variation in studies of shrubsteppe birds. Pages 154-172 in *Community ecology* (J. Diamond and T. Case, Eds.). Harper and Row, New York.
- WOOLER, R. D., AND J. C. COULSON. 1977. Factors affecting the age of first breeding of the Kittiwake, *Rissa tridactyla*. *Ibis* 119:339-349.
- YORIO, P., AND P. D. BOERSMA. 1994. Consequences of nest desertion and inattendance for Magellanic Penguin hatching success. *Auk* 111:215-218.

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