The Auk 114(4):638–645, 1997

NEST-SITE SELECTION IN SOUTH POLAR SKUAS: BALANCING NEST SAFETY AND ACCESS TO RESOURCES

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ABSTRACT.—Although South Polar Skuas (*Catharacta maccormicki*) are important predators of Adélie Penguin (*Pygoscelis adeliae*) eggs and chicks, skuas experience both reproductive costs and benefits when nesting near Adélie Penguins. We present a conceptual model to show that skua nest placement is based on two mechanisms: nest safety and access to penguins. Skua nests close to subcolonies of breeding penguins are likely to suffer greater egg loss due to egg trampling by penguins and predation by other skuas. However, skuas nesting near penguins potentially benefit from direct access to penguin eggs and chicks. Given these reproductive tradeoffs, skuas should exhibit an optimal nesting distance relative to penguin subcolonies. Skua pairs located at the optimal distance minimize egg loss while maximizing access to penguin eggs and chicks. During four breeding seasons we monitored skua nest placement relative to breeding penguins and recorded the fate of all skua eggs and chicks. The results supported the safety and access mechanisms of our model. Skua nests close to penguin subcolonies were unsafe and lost eggs more frequently than those farther away. Once hatched, chicks were more likely to fledge in nests closer to penguin subcolonies. Furthermore, skua pairs may assess the quality of their nest site and adjust nesting locations between years. During 1991, skuas whose eggs had failed to hatch in 1990 nested significantly farther from their 1990 nest location and chose safer nest sites than did skuas that had nested successfully in 1990. *Received 8 July 1996, accepted 10 April 1997.*

SOUTH POLAR SKUAS (*Catharacta maccormicki*) often breed near Adélie Penguin (*Pygoscelis adeliae*) colonies around the coast of Antarctica (Müller-Schwarze and Müller-Schwarze 1973, Trillmich 1978). Although it is well known that South Polar Skuas do not require penguin prey for successful reproduction (Young 1963a, b, 1994; Pietz 1987), predation on penguin eggs and chicks provides a substantial food resource for adult skuas and their offspring (Young 1963a, b, 1994; Spellerberg 1971; Mund and Miller 1995), and this food resource probably attracts skuas to penguin colonies. South Polar Skuas may nest around the perimeter of Adélie Penguin colonies (e.g. Cape Hallet; Trillmich 1978) or between groups or "subcolonies" within a penguin colony. The reproductive success of skuas is both hindered and facilitated by their association with penguins. Skuas that nest near penguins often are attacked by them. These attacks often result in the skua being driven from its nest and the penguin subsequently stepping on the skua eggs and breaking them (Young 1963a, 1994; this study). South Polar Skuas also are well-known predators on each other's eggs and chicks (Young 1963a, 1994; Spellerberg 1971). Despite these negative effects, skuas continue to nest near penguin subcolonies and often maintain foraging areas that contain breeding Adélie Penguins (Young 1963a, b, 1994; Trillmich 1978).

Because South Polar Skuas experience reproductive costs and benefits based on the distance of their nests to penguin subcolonies, we propose the following conceptual model of skua nest placement (see Fig. 1). Skuas should nest far enough from penguin subcolonies to gain some safety from nest trampling by penguins and predation by conspecifics, but close enough to have access to penguins for food. Skua reproductive success (i.e. number of young fledged) depends on: (1) the safety of a nest in terms of vulnerability to egg loss, and (2) access to penguin resources that the nesting location provides to skuas.

Skua nests close to a penguin subcolony (or near paths regularly used by penguins) are not as safe as those farther away. Therefore, the safety function has a positive slope relative to the distance from penguins (Fig. 1). Because the intensity of penguin traffic is greatest immediately adjacent to subcolonies, the safety function for skua nests should not be linear (Fig. 1). When nest safety is low, egg loss may

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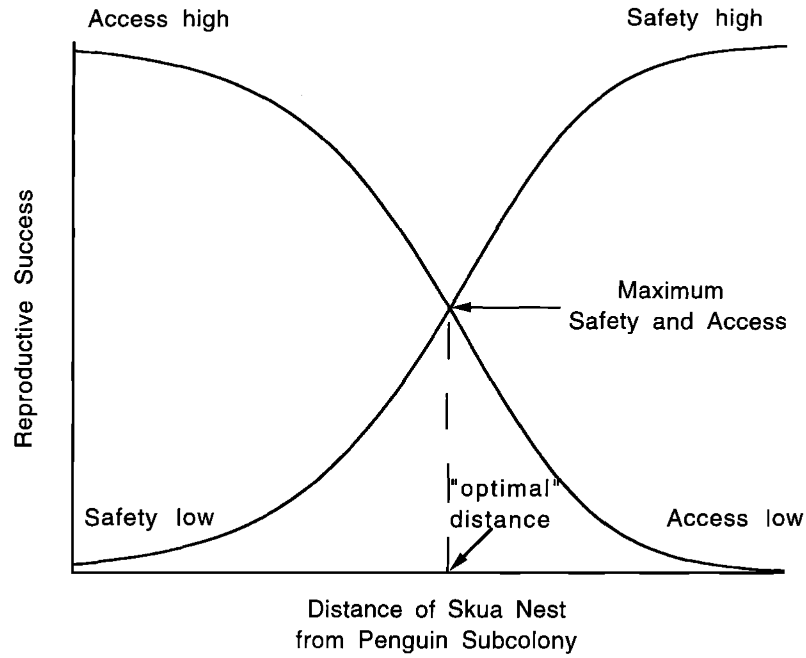

FIG. 1. Model of skua reproductive success (RS) relative to skua nest distance from penguin subcolonies. RS is determined by nest safety and access to penguins. The intersection of the safety and access regressions predicts the optimal skua nesting distance.

result from increased penguin traffic (G. D. Miller unpubl. data) and conspecific predation (Young 1994) near penguin subcolonies. In our model, egg loss is the primary factor limiting reproductive success of skua nests close to penguin subcolonies.

Skuas that nest close to penguins, however, have better access to high-quality food (i.e. penguin eggs and chicks) and potentially can protect their nests more easily (i.e. skuas forage within their nesting territory). Farther away from penguins, access to penguins for food declines. According to our model, restricted access to penguins is the primary factor limiting reproductive success when skuas nest away from penguin subcolonies (Fig. 1). This limitation is realized later in the breeding season when adult skuas are feeding chicks.

Assuming that nest safety and access to penguins are major factors affecting skua reproductive success, the model predicts that there will be an optimal distance from penguin subcolonies for skuas to place their nests (Fig. 1). At that distance, nest sites maximize both safety and resource availability and should exhibit the greatest reproductive success compared with the rest of the skua population. The optimal nesting distance is not absolute because the safety and access functions that determine the optimum may shift from year to year as the size and configuration of penguin subcolonies change, and as penguin traffic patterns shift because of snow drifts.

Using data collected during four field seasons from a color-banded population, we addressed several aspects of South Polar Skuas breeding in and around an Adélie Penguin colony at Cape Bird, Ross Island, Antarctica (77°13′S, 166°28′E). First, we followed the fates of eggs and chicks from all skua nests for evidence of a reproductive tradeoff. If safety is a problem for skuas primarily during incubation (when eggs are vulnerable to trampling by penguins and/or loss to conspecifics), then egg loss should be greater at nests that are closer to penguin subcolonies than at nests farther away. However, if access to penguin eggs and chicks is important to survival of skua chicks, then chicks hatching at nests close to a penguin subcolony should be more likely to fledge than are chicks hatching farther away. Second, we assessed overall reproductive success (number of chicks fledged) at skua nests. Our model predicts that reproductive success should exhibit an inverse parabolic relationship relative to distance from penguins, with a maximum point representing the optimal nesting distance (Fig. 1). Third, we analyzed nesting density of skuas relative to penguin subcolonies, and skua reproductive success relative to skua nest density. Finally, we monitored nest-site selection over two consecutive seasons to determine how banded pairs changed their nest location relative to the outcome of the previous year's breeding attempt.

Study Area and Methods

Study area.—Approximately 170 pairs of South Polar Skuas breed in association with 23,000 to 41,000 pairs of Adélie Penguins at the northern colony at Cape Bird (Taylor et al. 1990). No other skua or penguin species nests in the area. Nearly all of the skuas in this population were color-banded for individual identification. The penguin colony lies along 1.1 km of beach front and extends back from the beach for 100 to 500 m. The physical structure of the penguin colony is complex. Along the beach there is extensive flat ground, but back from the beach the terrain rises in stages to a steep moraine (ca. 250 m elevation). The higher ground is cut by several meltwater streams that create a series of gullies and ridges. The penguins nest in many dense subcolonies (distance between nests within a subcolony ca. 1.25 m) that cover most of the ground and end at the steeper slopes of the moraine. Penguin subcolonies range in size from a single pair to 1,000 pairs and are separated by open spaces. Skua nests are interspersed among subcolonies, around the perimeter of the penguin colony, and higher up on the moraine.

Measurements and reproductive success.—We chose distance to the nearest penguin nest as an objective index of safety and access. During the 1987, 1988, 1990, and 1991 breeding seasons, we measured the distance from each skua nest to the nearest penguin subcolony (the nearest penguin nest). In addition, as a measure of skua nesting density we measured the distance from a skua nest to its nearest and second nearest neighboring skua nests to assess the role of conspecifics on skua reproductive success.

South Polar Skuas typically lay two eggs. Daily nest checks determined laying date, egg losses, hatching date, and dates of chick death or fledging. If an egg disappeared, the nest and surrounding area were examined to determine cause of the loss. Penguin trampling typically left crushed debris in the nest scrape, whereas conspecific predators removed intact eggs from the scrape and left no traces. These categorizations came from 4,800 h of direct observations at nests in 1990 and 1991. Daily nest checks did not affect the reproductive success of skuas during the study period (Miller 1992).

All renesting attempts were excluded from analyses because success of late-hatched eggs presumably is affected by undesirable conditions late in the breeding season. Skuas attempted to renest 68 times during the four breeding seasons but fledged only six chicks. During 1991, more than one-third of the skua nests were excluded because they were used in other experimental manipulations. We excluded from analyses all skua nests that were more than 80 m from a penguin subcolony. These nests were on the top of the moraine or on isolated ridges and were not directly affected by the presence of penguins.

To obtain an estimate of skua nesting success relative to distance from penguin subcolonies, we analyzed skua nests in groups of 10. We used 10 nests to provide sufficient range in the number of offspring produced by groups, rather than 0, 1, or 2 offspring for an individual nest. Groups of 10 also removed any effect of skua nest density on fledging success. For each season, nests were sorted by their distance from penguin subcolonies and grouped consecutively (i.e. the 10 nests closest to penguin subcolonies formed the first group). Reproductive success (total number of chicks fledged) and the mean distance from penguins were calculated for each group. The distance at which skuas had the highest reproductive success was estimated using a best-fit quadratic regression and solving for its maximum point. Given the high nest and mate fidelity of skua pairs, a quadratic analysis of all years may overestimate the degrees of freedom, because each nest is not independent from year to year. Therefore, we analyzed each year separately, as well as all years combined, with the effect of year analyzed as a covariate.

We assessed reproductive failure on a per-egg basis by comparing the distance to penguins for eggs that were lost due to penguin trampling, eggs lost to conspecific predation, and eggs that hatched. Similarly, we compared the distance to penguins for chicks that fledged with chicks that did not fledge.

To assess the influence of neighboring skuas on reproductive success, we analyzed whether the number of chicks fledged at nests was related to skua nest density. Similar to the analyses of skua reproductive success versus distance to penguins, we sorted all the skua nests by their mean distance to their two skua neighbors. Then, by ordering nests in groups of 10, we examined the spatial patterns of reproductive success relative to the proximity of other skuas. This analysis was carried out for individual years and all years combined (with year as a covariate).

Finally, in order to examine the ability of skuas to assess their nesting location, we compared nest sites of skua pairs over two consecutive seasons. During 1990 and 1991, we assigned a "safety" code to all

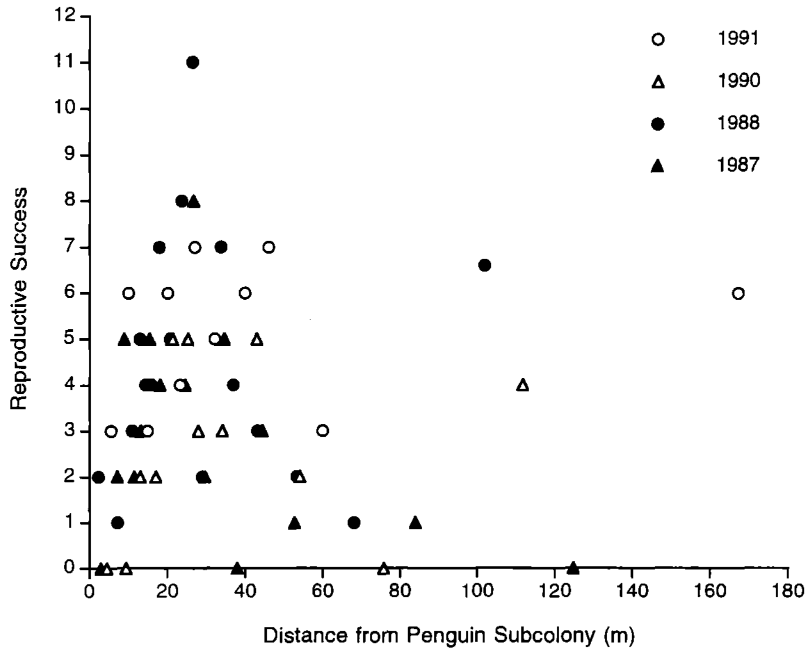

FIG. 2. Quadratic regressions of skua reproductive success (number of chicks fledged) vs. distance from skua nests to penguin subcolonies over four breeding seasons (see Table 1 for quadratic parameters). Each point represents a group of 10 nests.

skua nests. "Safety" was a qualitative assessment (0 to 4 scale) of nest location relative to penguin traffic. It considered the skua nest position relative to the nearest penguin subcolony, other nearby subcolonies, pathways frequented by penguins, and topographic features (e.g. boulders, ravines) that would shield a skua nest from destruction by penguins. A nest with safety = 0 experienced high penguin traffic, whereas a nest with safety = 4 had little chance of being affected by penguins. In 1991, we also measured the distance of each skua nest to the nest site used by that pair in the previous year, as well as the distance from the two nest sites to the nearest penguin subcolony. These measurements determined any patterns of nest movement. Nests were divided into pairs that failed in 1990 (no eggs hatched in 1990) and pairs that hatched at least one egg in 1990. We further divided the nests that hatched egg(s) in 1990 into those that succeeded in raising young and those that lost their chick(s). We used t-tests with unequal variance to examine the distances moved by these groups and paired t-tests to assess any differences in the distance from penguins between the two nesting sites. Finally, we used Wilcoxon matched-pairs signed-rank tests on nest-safety scores to determine if unsuccessful pairs in 1990 moved to safer sites in 1991.

RESULTS

Optimal nesting distance.—Quadratic regressions produced characteristic inverse parabolic curves of skua reproductive success relative to distance from penguin subcolonies (Fig. 2). The distance from penguin subcolonies accounted for 32 to 74% of the variation in reproductive success of skuas (Table 1). The distance that yielded maximum reproductive success in skuas varied between years (Table 1). In the quadratic analysis based on data from all years, the squared distance to penguins was a highly significant variable ($F = 22.93$, df = 1 and 46, $P < 0.0001$), and year was a significant covariate ($F = 3.09$, df = 3 and 46, $P = 0.04$). Interaction factors were not significant ($P > 0.13$).

When the distance to skua neighbors was used as the independent variable (using sorted groups of 10 nests) and regressed against reproductive success, no significant linear, quadratic, or cubic relationship existed for any individual year (F-tests, $P > 0.09$). However, when we combined data over all years, we found a significant linear relationship with a

TABLE 1. Quadratic regression parameters of South Polar Skua reproductive success versus distance from nests to a penguin subcolony.

Year	n	r^2	Optimal nesting distance (m)[a]	P
1987	15	0.32	27.9	0.080
1988	16	0.40	32.7	0.028
1990	11	0.74	36.0	0.005
1991	10	0.61	33.6	0.023
All years	52	0.41	31.1	0.0001

[a] Distance at which reproductive success was highest, as calculated from maximum point in quadratic equation.

slightly negative slope ($F = 5.33$, df = 50, $r^2 = 0.32$, slope = -0.05, $P = 0.001$). The mean distance to skua neighbors (i.e. nesting density) and year were significant variables in the model (distance: $F = 5.7$, df = 1 and 46, $P = 0.02$; year: $F = 5.21$, df = 3 and 46, $P = 0.004$); the interaction terms were not significant. The combined data set suggests that nests closer to other skuas were more productive than those farther from other skuas. The mean distance from a skua nest to its two nearest neighbors served as an estimate of territory size (i.e. it approximates the diameter of skua territories). The mean internest distance varied across seasons from 24.1 m in 1987 to 24.8 m in 1991.

For all seasons combined, there was no relationship between distance to nearest penguin subcolony and distance to nearest skua neighbor (F-test, $P > 0.05$). Therefore, skua nest densities were not higher closer to penguin subcolonies. When we analyzed the data separately by year, only 1991 was statistically significant ($F = 4.01$, df = 104, $P = 0.05$; all other years, $P > 0.19$). However, the slope of this line was close to zero (0.14), and the r^2 value (0.04) indicated that distance to penguins explained only 4% of the variation in skua nest density.

Patterns of reproductive success.—The distance to the nearest penguin subcolony did not differ between skua nests that lost eggs to penguin trampling and those that lost eggs to conspecific predation (Table 2). During three of four breeding seasons, however, skua eggs lost to either source were significantly closer to penguin subcolonies than were eggs that hatched (Table 2). Once eggs hatched, the reverse pattern occurred. Chicks fledged in nests that were significantly closer to penguin subcolonies in three of four years (Table 2).

Shifts in nest location following failure.—We followed 133 skua nests over two consecutive seasons (1990, 1991). In 122 (92%) of those nests, both individuals returned and nested within the same territory, but not necessarily at the same site. In the remaining 11 nests, one member of the 1990 pair was replaced in 1991 (new females in six nests, new males in five nests). In 63 cases we determined the distance between the new nest location (in 1991) and the old nest location (1990), and in 65 cases we documented safety codes of new and old sites. Skua pairs that hatched no eggs in 1990 moved their nests (within their territories) a greater distance in 1991 ($\bar{x} = 17.8$ m, $n = 24$) compared with skuas that hatched at least one egg in 1990 ($\bar{x} = 5.2$ m, $n = 39$; $t = 3.27$, df = 32, $P < 0.003$). In the process of moving within their territories, pairs that hatched no eggs also nested at safer sites in 1991 (Wilcoxon matched-pairs signed-rank test, $T = 175$, $n = 65$, $P < 0.03$). They did not, however, move their nests significantly closer to or farther from penguins (paired t-test, $P > 0.05$). Of the pairs that hatched at least one egg in 1990, those that failed to raise a chick did not move their nests farther from their previous

TABLE 2. Mean distance (m) from South Polar Skua nests to Adélie Penguin subcolonies and subsequent fate of associated skua eggs and chicks. Sample sizes are in parentheses.

Season	Eggs lost to[a]		Eggs hatched[b]	Chicks died	Chicks fledged[c]
	Penguins	Skuas			
1987	17.4 (20)	24.2 (101)	27.6 (142)*	30.3 (94)	22.1 (48)**
1988	17.5 (30)	21.2 (85)	31.3 (162)***	35.4 (92)	25.9 (70)**
1990	23.8 (29)	26.6 (54)	33.2 (76)**	35.2 (51)	29.4 (25)*
1991	18.9 (7)	29.6 (47)	31.7 (82)	30.4 (30)	32.5 (52)

*, $P < 0.05$; **, $P < 0.001$; ***, $P < 0.0001$.

[a] No significant difference ($P > 0.05$) between eggs lost to penguins and those lost to skuas.

[b] Kruskal-Wallis ANOVA comparing nests at which eggs hatched vs. nests at which eggs were lost to penguins or skuas.

[c] Mann-Whitney U-tests comparing nests at which chicks fledged vs. nests at which chicks died.

site than did pairs that fledged chicks (t-test, $P > 0.05$). Pairs that lost chicks also did not move their nest site any closer to or farther from the nearest penguin subcolony (paired t-test, $P > 0.05$).

Discussion

In support of our conceptual model of the spatial pattern of skua reproductive success, skua nests closest to penguin colonies were less productive, and reproductive success increased up to an optimal distance and then gradually declined farther from penguin subcolonies. The estimated optimal nest distance shifted approximately 8 m over the four years of study (Table 1). Changes in the optimal nesting distance may be related to changes in the penguin/skua nesting landscape, such as shifts in snowbanks that cause changes in penguin traffic, the presence or absence of small penguin subcolonies, or changes in skua territory sizes. High annual variation in skua reproductive success at Cape Bird (Miller 1992) probably caused year to be a significant cofactor in the quadratic regression based on the entire data set.

The few skua nests located outside the influence of the penguin colony (>80 m) experienced variable reproductive success (Fig. 2). Reproductive success was relatively high in three of four years, suggesting that nests located far from penguins were safe from trampling by penguins and had lower levels of predation by conspecifics (Table 2). However, these nests did not experience higher reproductive success than that at the optimal distance from penguin subcolonies (Fig. 2).

The main peak in skua reproductive success is consistent with reproductive tradeoffs relative to the proximity of nests to penguin subcolonies. We propose two mechanisms governing skua success: egg safety and access to penguins. These mechanisms were supported by the outcomes of skua breeding attempts (Table 2). Eggs were more likely to be lost in nests closer to penguin subcolonies than in nests farther away. Once hatched, however, more chicks fledged in nests closer to penguin subcolonies, providing support for the access mechanism. We suggest that chick survival is enhanced closer to penguins because of greater access to penguin eggs and chicks. Furthermore, foraging near their nest sites may allow adult skuas to protect their chicks from conspecific predation. Studies that determine the diets and causes of mortality (e.g. starvation or predation) of skua chicks are needed to understand the relationship between skua reproductive success and the presence of penguins.

We also suggest that skua pairs are capable of shifting their nests to more favorable locations following a failed breeding season. Skua pairs that hatched no eggs in 1990 moved their 1991 nesting sites farther from their previous sites and to safer locations (e.g. by rocks or away from penguin pathways) compared with pairs that hatched at least one egg in 1990. Several mechanisms may allow skuas to assess their breeding situation prior to nesting. First, skuas arrive approximately three weeks after the arrival of penguins and spend about two weeks in the area before nesting. Second, most pairs return to the same territory each year and prepare several potential nest scrapes before settling on one (G. D. Miller pers. obs.). We found no evidence, however, that skuas are able to fine-tune their placement of nests relative to penguin subcolonies. For example, pairs that lost young in 1990 did not move their nests closer to penguins, in order to increase access to the subcolony. Given that skuas return to breed at the same location each year, the distance that a pair can shift may be constrained by the size of the breeding territory and its overall location relative to penguins. We would predict, however, that the most favored skua territories are closest to the optimal nesting distance (ca. 30 m) from penguins.

In some years, penguins caused up to 29% of all skua egg losses (G. D. Miller unpubl. data). The negative influence of a prey species on its predator occurs among assemblages of insects, fish (Polis et al. 1990), and some colonial birds (Gilchrist et al. 1994). Most predators that attack relatively large prey must weigh the risks of injury against the likelihood of a successful attack. The destruction of skua nests by penguins is analogous to a prey species acting as a predator. From a behavioral standpoint, however, the situation is unique because penguins are not acting as predators (i.e. they do not eat skua eggs or chicks). Instead, they attack adult skuas at their nests. When a skua dodges an attacking penguin, the penguin often walks into the skua's nest and tramples the eggs. Normally, penguins do not appear to be interested in the eggs directly, but occasionally they puncture skua eggs that are left unattended (Young 1994). As a consequence, our conceptual model and results may be limited to fairly specific conditions with colonial birds where the vulnerability of the predator is determined directly by nest placement. Among other nesting assemblages of birds, predator and prey may benefit from each other (e.g. Wilklund 1979, 1982). Alternatively, the association between predator and prey may be neutral for the predator and beneficial only for the prey species (Wheelwright et al. 1997).

Intraspecific predation on eggs is commonplace among skuas (Young 1963a, 1994) and can account for up to 71% of all egg losses (G. D. Miller unpubl. data). Like penguin trampling, egg loss to conspecifics was more likely to occur in skua nests that were closer to penguin subcolonies (Table 2). Increased intraspecific predation near penguins was not due to skua nest density, however, because skua nest densities were not higher near penguin colonies. Egg loss may have resulted from greater skua traffic near penguin subcolonies because skuas were attracted to the penguin food source.

Clearly, nest safety and access to penguins are not the only factors affecting skua reproductive success. Reproductive success increased slightly when skuas nested closer to one another. In contrast, most skua nests experienced fairly large changes in reproductive success relative to their distance from penguin subcolonies (Fig. 2). The slight increase in reproductive success at nests closer to other skua nests may have resulted from increased protection that comes from colonial breeding (Wilklund and Andersson 1980). It also may indicate that skuas prefer to nest in certain areas based on particular microhabitat characteristics. Away from the main breeding area, skua nests may have been more exposed to wind or subjected to flooding, both of which are likely to cause nest failure (Young 1994).

Other factors such as longevity and strong territory and mate fidelity (Ainley et al. 1990, Pietz and Parmelee 1994, Young 1994) may confound patterns of reproductive success in skuas. In Great Skuas (*Catharacta skua*), for example, fledging success is higher for experienced pairs than for first-time breeders (Furness 1984). Laying date also affects success because late-hatched eggs and chicks may be more likely to experience adverse weather, and the provisioning ability of parents may decrease as food becomes less abundant (Trivelpiece and Volkman 1982, Nielson 1983 *in* Pietz 1987). Finally, if younger, less-experienced skuas are forced to use particular areas around penguin colonies, this could have affected our results. We could not address age-related issues directly because we did not have enough known-age birds in our study population.

In order to make objective measurements of the safety and access mechanisms used in our conceptual model, we used the distance of each skua nest to the nearest penguin subcolony. It is important to note, however, that neither safety from nor access to penguins is entirely dependent on the distance between skua nests and penguin subcolonies. Some skua nests that are close to penguins may be quite safe from penguins (e.g. a skua nest sheltered by a boulder). Similarly, it is not clear that a skua's access to penguins is directly related to distance. Access to penguin prey may be graded by the number of skua territories between a skua nest and the nearest penguins. The number of penguin nests within a skua's foraging area also may approximate the availability of penguin food. Finally, the importance of penguins in the diet varies among skuas, and many skua pairs eat more fish than penguins (Young 1994). We could not assess diets of skuas in this study. However, several lines of evidence have shown that even skuas with no penguin nests within their territories feed on penguin eggs and chicks (Mund and Miller 1995). Apparently, penguin prey is sought after regardless of how far skuas nest from penguins.

Young (1994) suggested that South Polar Skuas benefit little by nesting near Adélie Penguins, and that the association of penguins and skuas is driven more by abiotic factors (i.e. nest microclimate). Yet, despite the multiple variables that potentially influence skua reproductive success, it is striking that one measure in particular, distance from a skua nest to a penguin subcolony, explains a large amount of the spatial variation in reproductive success in our study. Other investigators have reported that the distribution of South Polar Skua nests is influenced by the presence of penguins (Müller-Schwarze and Müller-Schwarze 1973, Trillmich

1978). We provide direct evidence of the negative effect, via egg loss, that skuas experience when nesting near penguins. Furthermore, the patterns of survival of skua chicks are correlated with the access mechanism that we propose. Based on these results, we argue that the association of penguins and skuas is neither coincidental nor benign. Presumably, skuas must benefit from nesting near penguins in order to balance a measurable cost to their reproductive success. Clearly, additional work is needed to more fully understand the interactions between nesting penguins and skuas.

Acknowledgments

Field work for this project was funded by NSF grants INT-8603504 and DPP-8916333 to G.D.M. and New Zealand University Grants Committee funding to G.D.M. and G. S. Court. The New Zealand Antarctic Programme and the U.S. Antarctic Program furnished logistic support. We thank D. Hutchinson, R. Wilson, K. Nordin, A. McKechnie, B. Keimel, P. Martin, G. Wallace, and E. Speirs for their assistance in the field. A special thank you to Dr. J. Brown who gave helpful suggestions during synthesis and write-up and to Dr. E. Bedrick for his statistical advice. Dr. E Toolson, M. J. Mund, and Dr. M. Merola also added useful insights during data interpretation. Drs. K. Martin, T. Martin, and P. Pietz gave helpful comments on earlier versions of the manuscript. Funding for J.C.H. was provided by an NSF Predoctoral Fellowship.

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Associate Editor: K. Martin