*The Condor* 94:598–607

# INTRACOLONY VARIABILITY DURING PERIODS OF POOR REPRODUCTIVE PERFORMANCE AT A GLAUCOUS-WINGED GULL COLONY[1]

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*Abstract.* We studied intracolony variability in habitat attributes of nest sites and breeding performance in two years when average breeding success was poor at a colony of Glaucous-winged Gulls (*Larus glaucescens*) in southcoastal Alaska. There were few significant relationships between habitat attributes of nest sites and either breeding chronology or breeding success within four island-year samples, and none were consistent among samples. Hatching success (number of eggs hatching/number of eggs laid) was strongly and positively related to clutch size. Differences in reproductive performance among pairs were accentuated during periods of apparent stress, indicating that differences in parental quality expressed during favorable periods were amplified during unfavorable periods. These results contradict hypotheses that intrapopulation variability in clutch size represents adaptive adjustments of pairs based on their relative parenting ability or that pairs laying relatively large clutches are most adversely affected in bad years. Differences in reproductive performance seemed to persist between years. In 1979, when relatively few gulls bred, some areas of the colony contained no nests with eggs. In 1980, breeding chronology and performance until hatching did not differ between those areas and areas where gulls also bred in 1979, but fledging success was significantly lower in those areas than in areas where gulls also had nested in 1979.

*Key words: Reproductive failures; clutch size; individual quality; Glaucous-winged Gull;* Larus glaucescens.

## INTRODUCTION

Breeding performance of *Larus* generally is limited by foraging opportunities away from colonies (e.g., Hiom et al. 1991). However, even in such situations, habitat characteristics of breeding territories may constrain diet choice and influence within-colony variability in reproductive performance (Pierotti and Annett 1991). Indeed, numerous factors at colonies themselves can contribute to intracolony variability in reproductive success of gulls. Such factors may include physical characteristics of territories (Pierotti 1982, Pugesek and Diem 1983), nest spacing (e.g., Vermeer 1963, Buttler and Trivelpiece 1981), frequency of agonistic interactions (Butler and Janes-Butler 1982, Pierotti 1987), location within the colony (Coulson 1968, Dexheimer and Southern 1974, but see Ryder and Ryder 1981), and age or experience of breeding pairs (e.g., Coulson 1966, Davis 1975, Haymes and Blokpoel 1980, Pugesek 1983, Reid 1988, Pyle et al. 1991). The effect of such factors may vary in different ecological conditions, and their influence may be markedly different during periods of environmental stress than during generally favorable periods.

We (Murphy et al. 1984) previously reported poor breeding performance of Glaucous-winged Gulls (*Larus glaucescens*) in two years at a small colony in Alaska; in both years many pairs failed, but the timing of the failures differed between years. Predominance of mussels (*Mytilus edulis*) in the diet during the pre-nesting period through egg-laying in the first year and during the incubation and chick periods in the second year coincided with reproductive failures of many pairs. Here we examine attributes of nest sites and territories that potentially could differentiate successful from unsuccessful pairs within the colony in those two years when colony-wide reproduction was poor but some pairs were successful.

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[1] Received 23 April 1991. Accepted 4 March 1992.

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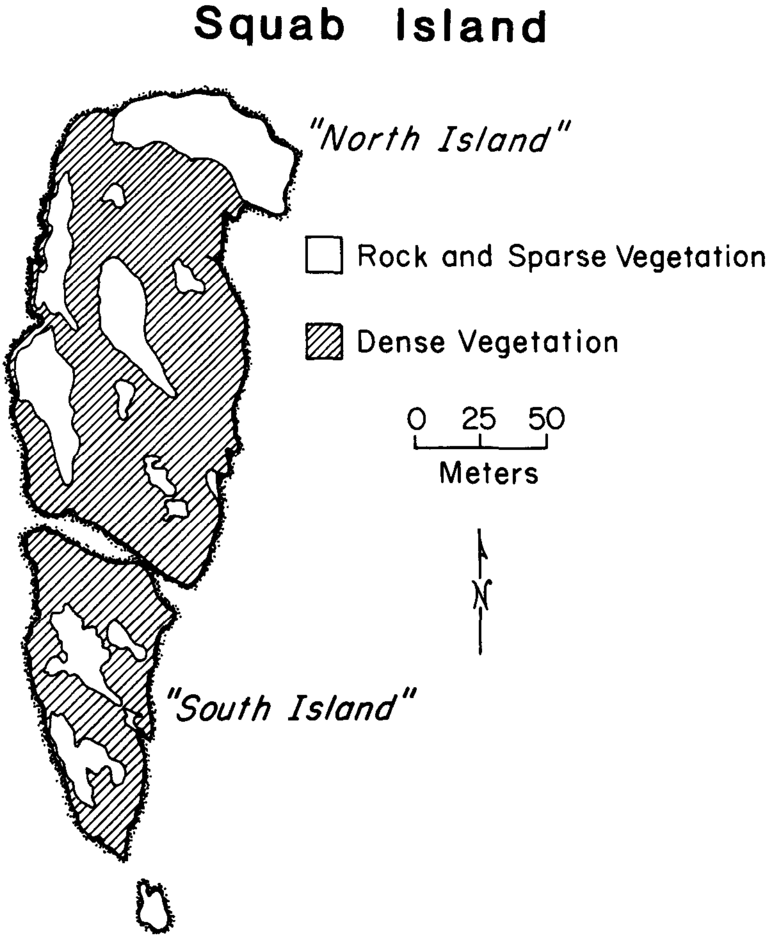

FIGURE 1. General habitat features of Squab Island, Alaska. A narrow fissure effectively divides the island into two parts at high tide, separating the areas referenced as "North Island" and "South Island."

Intercolony variability in clutch size may represent adaptive adjustments of individual pairs to raise as many fledglings as their ability permits (Högstedt 1980). Alternatively, in unfavorable periods those pairs that have produced relatively small clutches may be favored (Boyce and Perrins 1987). We examine the relevance of both of these hypotheses to patterns of intracolony variability in reproductive success by evaluating the relationships of hatching and breeding success to clutch size and of fledging success to initial brood size.

## STUDY AREA

Squab Island (59°56′N, 149°43′W) is approximately 50 m by 300 m in area and is located in the upper end of Aialik Bay, a heavily glaciated fjord in southcoastal Alaska. Inaccessible cliffs form the western side of the island, and steep slopes characterize the eastern side. Both high and flat, as well as low and very steep, portions of the island are unvegetated. Umbels (principally *Heracleum lanatum* and *Angelica lucida*) and grasses (*Poaceae*) dominate the vegetation, which is particularly lush on the lower, flatter portions of the island. In late May, when the gulls begin to nest, relatively little of the current year's vegetative growth has occurred. Well before the time of fledging (late July and early August), the current year's growth is fully-developed. The island is divided into two parts, hereafter "North Island" and "South Island," by a deep crevice about 185 m from the northern end (Fig. 1). The maximal elevation of North Island is about 40 m above mean lower low water (MLLW), and that of South Island is about 25 m.

## METHODS

Our visits to the island were one to several days apart between the pre-egg stage and the completion of fledging. Collection of data on reproductive chronology and output in 1979 and 1980 has been described in detail elsewhere (Murphy et al. 1984). We defined an active nest site as one where a nest was built and at least one egg was laid. We marked active nest sites with numbered tongue depressors within each season, but we were required by the National Park Service to remove the markers at the end of each season. Nest scrapes or partially-built nests were not marked or counted. Eggs were marked when first found. Chicks were individually marked when first found and counted on each territory on each visit. Once all active nests (nests with eggs) were found, we plotted the location of each active nest on a hand-drawn map of the island and measured the distance to the nearest active nest ("nearest-neighbor distance") to the nearest 0.1 m in the field. We measured several physical attributes of active nest sites, including elevation in meters above MLLW, aspect in relation to true north, and slope in degrees. No known-elevation landmarks were available to observers, and elevations were estimated independently each year. We classified the nest substrate as either (1) soil ($\leq$25% rock cover), (2) rock/soil, or (3) rock ($\geq$75% rock cover). Late in the chick period in each year, we estimated the composition of the vegetative overstory within a 1-m circle centered on each active nest. We estimated percent cover of unvegetated area, umbels, beach rye (*Elymus arenarius*), other grasses, and other vegetation.

We analyzed each island-year sample (North Island 1979, South Island 1979, North Island 1980, South Island 1980) separately. Frequency distributions of virtually all reproductive and habitat variables departed significantly ($P < 0.05$) from normality, generally precluding the use of univariate or multivariate parametric statistics. Frequency distributions of elevation, slope, nearest-neighbor distance, and initiation dates of clutches could be normalized by common log transformations; we used log-transformed values of these variables in all parametric analyses.

We examined relationships of nearest-neighbor distance and reproductive variables (initiation date of clutch, clutch size, number hatching/nest, number fledging/nest) to both substrate type and aspect using the Kruskal-Wallis test. For these analyses, we grouped aspect values into the four compass quadrants (North, East, South, West).

We initially examined relationships between each overstory cover variable and nearest-neighbor distance and reproductive variables using contingency tables and testing for row by column independence (Conover 1980). To conduct these analyses, we condensed the values of the overstory cover variables into five categories, ranging from 1 (0%), 2 (1–25%), and up to 5 (76–100%). These values were condensed further into three categories, ranging from 1 (absent), 2 (1–50%), to 3 (51–100%), if expected cell sizes using the five categories were small and violated the rules for minimal expected cell sizes in Chi-square analyses (see Conover 1980). We divided the frequency distributions of values for nearest-neighbor distance and clutch initiation date into quartiles for each island-year sample. For hatching (and fledging), we divided attempts into two categories: those that produced one or more hatched eggs (or fledged chicks) and those that failed before hatching (or fledging). For each of the four reproductive variables, this set of analyses produced 24 contingency tables (six habitat variables times four samples). We therefore used the Bonferroni method, dividing $\alpha$ by the number of tests (e.g., Beal and Khamis 1991), to determine the $\alpha$-level to use as a criterion for rejecting each null hypothesis of independence. We also used this method of adjusting $\alpha$ in the other sets of univariate analyses we report below.

After failing to find few significant relationships within samples and any consistent relationships among samples between any overstory cover variable and either nearest-neighbor distance or any reproductive variable (see below), we summarized variation in the five cover variables using a Principal Component Analysis on the variance-covariance matrix of those variables for each island-year sample. We then used each nest site's score on the first Principal Component axis (PC I) as a summary statistic for overstory cover at that nest site in subsequent analyses.

Following univariate analyses of relationships of nearest-neighbor distance and reproductive variables to habitat attributes of nest sites, we conducted multivariate analyses to examine combined influences of the habitat variables. We used stepwise multiple regression (Dixon et al. 1990: BMDP2R) to examine relationships be-

TABLE 1. Loadings of vegetative cover variables of Glaucous-winged Gull nest sites at Squab Island in 1979 and 1980 on the first Principal Component factor.

| | Year | | | |
|---|---|---|---|---|
| | 1979 | | 1980 | |
| | Island | | Island | |
| Percent cover | North | South | North | South |
| Open | −26.605 | −10.366 | −3.384 | −4.514 |
| *Heracleum*/*Angelica* | 37.362 | 33.488 | 35.516 | 40.569 |
| *Elymus* | −4.339 | −21.259 | −2.131 | −16.078 |
| Other grasses | −6.423 | −1.078 | −29.567 | −19.325 |
| Other taxa | 0.000 | −0.785 | −0.435 | −0.652 |
| Variance explained (%) | 63.4 | 51.8 | 59.6 | 44.4 |

tween nearest-neighbor distance and interval-scale habitat variables (elevation, slope, and PC I). For reproductive success, we classified attempts into two categories: those that produced one or more fledglings and those that produced no fledglings. We examined relationships of this measure of "nest success" to habitat variables (including nearest-neighbor distance) using stepwise logistic regression (Dixon et al. 1990: BMDPLR), specifying nest substrate and aspect (quadrant) as categorical variables and elevation, slope, PC I, and nearest-neighbor distance as interval-scale variables.

We further examined the relationship between attributes of nest sites and reproductive success by considering location on North Island. The number of active nests increased markedly on North Island between 1979 (150 nests) and 1980 (393 nests), but nearest-neighbor distances were equal in both years, indicating far more extensive nesting on that island in 1980 than in 1979 (Murphy et al. 1984). By overlaying hand-drawn maps of active nests on North Island in 1979 and 1980, we differentiated between areas of the island that contained active nests only in 1980 and those that contained active nests in both years. A total of 259 nests could be unequivocally assigned to one of these two "location codes." Because boundaries among nesting areas could not be delineated as well on South Island and the increase in the number of nests (130 to 180) was not as pronounced there as on North Island, such categorization was not possible for South Island. The analyses of location and reproductive success therefore are limited to North Island.

## RESULTS AND DISCUSSION

### VEGETATIVE COVER

Principal component analyses of the five cover variables for the four samples produced a synthetic variable (PC I) that summarized a contrast between the amount of *Heracleum* and *Angelica* cover and the amount of either open ground (North Island 1979), *Elymus* (North Island 1980), other grasses (South Island 1979), or both *Elymus* and other grasses (South Island 1980); high positive scores were associated with high percentages of *Heracleum* and *Angelica* cover in all four samples (Table 1). Factor loadings on PC I for each sample were used to calculate PC I scores for each nest site within each sample; the score is used as a summary measure of the five overstory cover variables for each nest site.

### NEST SITE CHARACTERISTICS AND NEST SPACING

In all four island-year samples nest densities were high and equaled or exceeded those reported for Glaucous-winged Gulls elsewhere (see Murphy et al. 1984). Hunt and Hunt (1976) documented an inverse relationship between nest densities and reproductive success in Glaucous-winged Gulls. Therefore, before examining the relationships between habitat features of nest sites and reproductive success, we examined relationships between each habitat variable and nest spacing. Based on analyses of contingency tables, distance to the nearest active nest showed no consistent relationship with aspect, substrate type, or any single measure of vegetative cover (Table 2).

To examine relationships between nearest-neighbor distance and elevation, slope, and vegetative cover score (PC I), we calculated regression equations and product-moment correlation coefficients (Table 2). Nearest-neighbor distances were significantly and negatively correlated with elevation in all island-year samples except South Island 1979; i.e., nests generally were more widely spaced at lower elevations except in that

TABLE 2. Relationships between nearest-neighbor distance (NND) and characteristics of nest sites of Glaucous-winged Gulls on Squab Island in 1979 and 1980 test results.

| | Year | | | |
|---|---|---|---|---|
| | 1979 | | 1980 | |
| | Island | | Island | |
| Habitat variable | North | South | North | South |
| Aspect[a] | 1.94 (3) | 5.60 (3) | 14.82 (3)** | 5.94 (3) |
| Substrate type[a] | 0.08 (2) | 0.17 (2) | 1.55 (2) | 9.18 (2)* |
| % open[b] | 2.813 (6) | 6.199 (6) | 2.125 (6) | 3.746 (6) |
| % *Heracleum* or *Angelica*[b] | 6.086 (6) | 2.860 (6) | 2.817 (6) | 10.326 (6) |
| % *Elymus*[b] | 12.061 (6) | 4.962 (6) | 7.124 (6) | 8.697 (6) |
| % other grasses[b] | 2.354 (6) | 2.307 (6) | 14.264 (6) | 6.915 (6) |
| Elevation[c] | −0.325 (120)** | −0.033 (112) | −0.271 (382)** | −0.313 (184)** |
| Slope[c] | 0.008 (120) | 0.007 (112) | 0.186 (382)** | 0.234 (184)** |
| PC I[c] | 0.133 (120) | 0.040 (112) | 0.023 (372) | −0.002 (181) |

[a] Kruskal-Wallis test, Chi square test statistic (degrees of freedom).
[b] Chi square test for independence (degrees of freedom).
[c] Correlation coefficient (degrees of freedom).
*$P < 0.05$
**$P < 0.005$

sample. In both 1980 samples, but in neither 1979 sample, nearest-neighbor distance was positively and significantly correlated with slope; i.e., in 1980, nests on steeper slopes were spaced farther apart. Nearest-neighbor distances were unrelated to PC I in all four samples (Table 2).

To examine the multivariate relationships of nearest-neighbor distance to elevation, slope, and PC I, we conducted a separate stepwise multiple regression analysis for each island-year sample, specifying elevation, slope, and PC I as independent variables and nearest-neighbor distance as the dependent variable. None of the variables accounted for significant ($P < 0.05$) variability in nearest-neighbor distances in the South Island 1979 sample. Elevation entered the model first for each of the other three samples, accounting for 6.6 (North Island 1980) to 10.5 percent (North Island 1979) of the variation in nearest-neighbor distance. After elevation had entered the model, slope accounted for significant ($P < 0.05$) residual variation in nearest-neighbor distance only in the North Island 1980 sample. PC I did not contribute significantly to any of the four models. Thus, for the 1980 North Island sample, nests were spaced farthest apart on steep slopes and at low elevations and were closest on gentle slopes at high elevations.

For each island-year sample, we constructed a series of two-way contingency tables to examine relationships between aspect, substrate type, and the overstory cover variables (excluding "other," which occurred infrequently) and four reproductive variables (initiation date of laying, clutch size, hatching, and fledging). Using the Bonferroni method, we used an $\alpha$ of 0.002 (0.05/24) as our criterion for rejecting each hypothesis of independence. Only one of the analyses was significant (clutch size vs. "other grasses," North Island 1980). These analyses indicated that reproductive performance generally was unrelated to these nest site characteristics within samples; additionally, there were no significant relationships, even at $\alpha = 0.05$, that were consistent among samples.

To examine relationships between each continuous habitat variable (elevation, slope, PC I, and nearest-neighbor distance) and each of the four measures of reproductive performance, we produced bivariate plots to check for nonlinearities and calculated product-moment correlation coefficients and least squares regression coefficients. Based on the Bonferroni method, we used $\alpha = 0.003$ (0.05/16) to assess statistical significance. No correlations were significant using this criterion. Thus, none of these habitat variables accounted for variability in these four measures of reproductive performance within any of the four island-year samples.

To examine the combined effects of nest site characteristics on nest success (no fledglings produced vs. one or more fledglings produced), we used stepwise logistic regression, specifying elevation, slope, PC I, and nearest-neighbor distance as continuous independent variables and aspect (compass quadrant) and substrate type as categorical independent variables. For the North Island 1979 sample, nest success was significantly ($P < 0.05$) related to both substrate type and PC I; however, once substrate type had first entered

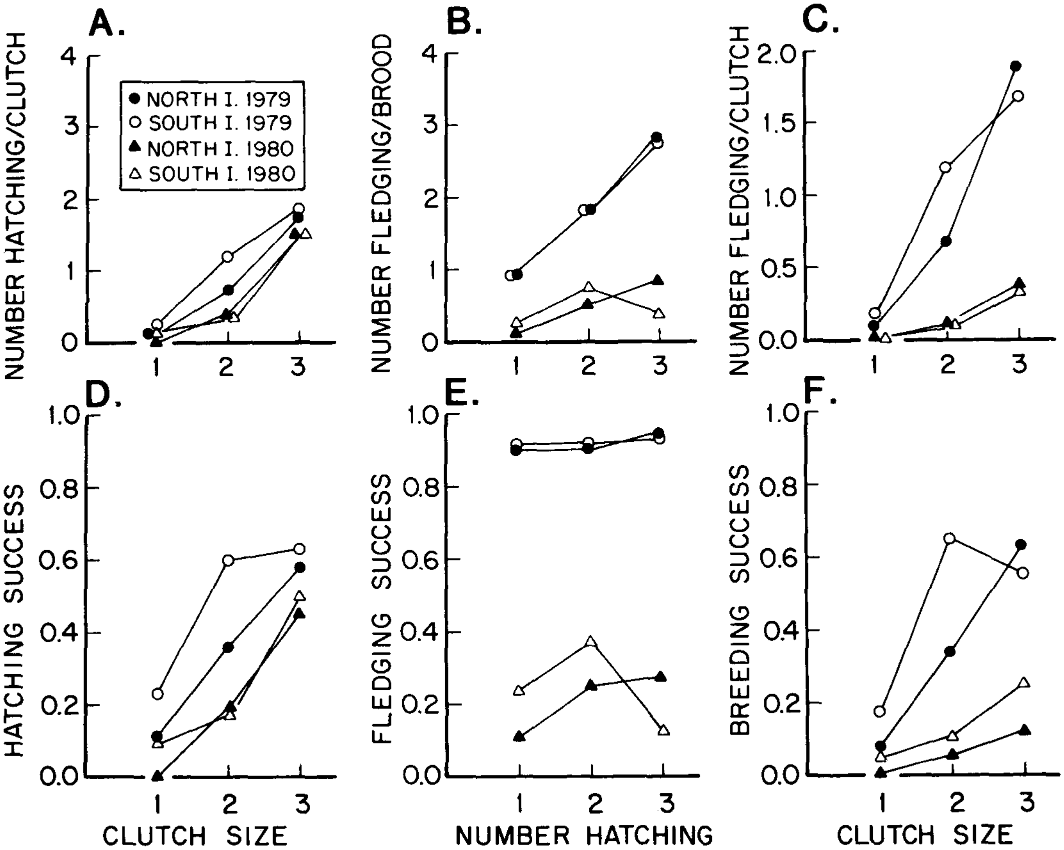

FIGURE 2. Relationships of reproductive success to clutch size and the number of eggs hatching/clutch.

the model, no other variables, including PC I, significantly ($P < 0.05$) improved the model. On the basis of substrate type, nest success of 64 percent of the attempts was classified correctly for this sample. Nest success was not significantly ($P < 0.05$) related to any of the nest site characteristics in any of the other three samples. Thus, the multivariate results confirm the univariate results of few significant relationships within samples and no consistent relationships among samples between habitat attributes of nest sites and any measure of reproductive performance.

## PREVIOUS PERFORMANCE AND REPRODUCTIVE SUCCESS

Differences in individual "quality," whether related to age, experience, or other factors, could account for variability in reproductive success within each island-year sample. Because we did not physically examine adults, we have no direct measures of condition or other variables that could affect reproductive performance. We therefore examined the relationship between "quality" and reproductive success in two indirect ways. First, we examined the relationships of clutch initiation date, hatching success, and breeding success to clutch size and of fledging success to initial brood size for each island-year sample. Second, we divided the North Island 1980 sample into two "location code" categories: nests in areas where adults also actively nested in 1979 and nests in areas where no pairs had produced clutches in 1979. It is likely that the former category was composed primarily of adults that had bred in 1979 and the latter of adults that failed to initiate clutches in 1979.

The number of eggs hatching/clutch was positively related to clutch size in all four samples (Fig. 2). Hatching success (number of eggs hatching/number of eggs laid) also was positively related to clutch size (Table 3, Fig. 2); i.e., the probability that eggs would hatch was positively related to clutch size in all four samples. The number fledging/brood was positively related

TABLE 3. Relationships of breeding chronology, hatching success, and breeding success to clutch or brood size of Glaucous-winged Gulls on Squab Island in 1979 and 1980.

| | | Year | | | |
|---|---|---|---|---|---|
| | | 1979 | | 1980 | |
| | | Island | | Island | |
| Variable | Clutch or brood size[a] | North | South | North | South |
| Initiation date | 1 | 2 June ± 6 days (33)[b] | 1 June ± 5 days (12) | 5 June ± 7 days (22) | 2 June ± 7 days (20) |
| | 2 | 30 May ± 5 days (17) | 31 May ± 1 day (6) | 2 June ± 5 days (63) | 4 June ± 5 days (29) |
| | 3 | 1 June ± 4 days (6) | 31 May ± 0 days (4) | 30 May ± 4 days (148) | 30 May ± 4 days (67) |
| | Comparison[c] | 1 = 2 = 3 | 1 = 2 = 3 | (1 = 2) > 3 | 2 > 3 |
| Hatching success | 1 | 0.11 ± 0.31 (38) | 0.23 ± 0.43 (26) | 0.00 (22) | 0.09 ± 0.29 (22) |
| | 2 | 0.36 ± 0.46 (42) | 0.60 ± 0.44 (46) | 0.20 ± 0.36 (100) | 0.17 ± 0.35 (46) |
| | 3 | 0.58 ± 0.39 (38) | 0.62 ± 0.39 (39) | 0.49 ± 0.43 (260) | 0.50 ± 0.43 (116) |
| | Comparison | 1 < 2 < 3 | 1 < (2 = 3) | (1 = 2) < 3 | (1 = 2) < 3 |
| Breeding success | 1 | 0.08 ± 0.28 (37) | 0.17 ± 0.39 (23) | 0.00 (22) | 0.00 (21) |
| | 2 | 0.34 ± 0.46 (37) | 0.64 ± 0.45 (35) | 0.05 ± 0.18 (99) | 0.04 ± 0.18 (46) |
| | 3 | 0.63 ± 0.37 (26) | 0.55 ± 0.40 (29) | 0.12 ± 0.23 (257) | 0.10 ± 0.19 (116) |
| | Comparison | 1 < 2 < 3 | 1 < (2 = 3) | (1 = 2) < 3 | (1 = 2) < 3 |
| Fleding success | 1 | 0.90 ± 0.32 (10) | 0.91 ± 0.30 (11) | 0.11 ± 0.31 (38) | 0.24 ± 0.44 (17) |
| | 2 | 0.91 ± 0.30 (21) | 0.91 ± 0.19 (29) | 0.25 ± 0.33 (65) | 0.37 ± 0.40 (34) |
| | 3 | 0.94 ± 0.13 (12) | 0.92 ± 0.15 (13) | 0.27 ± 0.30 (82) | 0.12 ± 0.20 (39) |
| | Comparison | 1 = 2 = 3 | 1 = 2 = 3 | 1 < (2 = 3) | 2 > 3 |

[a] Clutch size for initiation date, hatching success, and breeding success; number hatching for fledging success.

[b] Mean ± standard deviation (sample size).

[c] Pairwise comparison procedure (see Dixon et al. 1990:578). Inequalities are denoted if $P < 0.05$ for the overall Kruskal-Wallis test statistic and that comparison.

TABLE 4. Reproductive output and habitat attributes of nest sites of Glaucous-winged Gulls in different locations on North Island in 1980.

| Variable | Areas used in 1979 and in 1980 | Areas not used in 1979 | P[a] |
|---|---|---|---|
| Initiation date | 31 May ± 5 days (75) | 1 June ± 5 days (79) | 0.138 |
| Clutch size | 2.65 ± 0.59 (118) | 2.67 ± 0.57 (141) | 0.898 |
| Number hatching/clutch | 1.26 ± 1.32 (118) | 1.12 ± 1.23 (141) | 0.379 |
| Number fledgings/clutch | 0.36 ± 0.64 (118) | 0.22 ± 0.59 (139) | 0.010 |
| Elevation (m) | 29.3 ± 3.8 (118) | 25.0 ± 5.3 (141) | <0.001 |
| Slope (degrees) | 11.7 ± 8.6 (118) | 16.8 ± 10.7 (141) | <0.001 |
| Unvegetated (%) | 7.2 ± 18.9 (115) | 2.5 ± 10.4 (137) | 0.008 |
| *Heracleum* (%) | 40.6 ± 37.0 (115) | 56.4 ± 38.7 (137) | 0.001 |
| *Elymus* (%) | 10.3 ± 25.2 (115) | 9.4 ± 27.2 (137) | 0.404 |
| Misc. grasses (%) | 39.8 ± 35.2 (115) | 29.4 ± 33.5 (137) | 0.012 |
| Misc. vegetation (%) | 2.1 ± 7.9 (115) | 2.4 ± 12.9 (137) | 0.289 |
| PC I[b] | 220 ± 2,142 (115) | 1,106 ± 2,169 (137) | 0.002 |
| Nearest-neighbor distance (m) | 2.93 ± 1.21 (118) | 3.84 ± 1.86 (141) | <0.001 |

[a] Mann-Whitney test.
[b] See text.

to initial brood size (number of eggs hatching) in three of the four samples, but was highest for broods of two and lowest for broods of three in the South Island 1980 sample (Fig. 2). Fledging success was unrelated to initial brood size in the two 1979 samples. Fledging success was higher for two-chick and three-chick broods than for single-chick broods in the North Island 1980 sample. However, in the South Island 1980 sample, fledging success was higher for two-chick broods than for three-chick broods. This is the only instance when a smaller clutch or brood outperformed a larger one (Table 3, Fig. 2). The number fledglings/clutch was positively related to clutch size in all four samples (Fig. 2). In general, breeding success (number of fledglings/clutch size) was positively related to clutch size (Fig. 2); in 1980, when clutches of three eggs predominated, no one-egg clutches produced any fledglings and two-egg clutches produced significantly fewer fledglings than did three-egg clutches on a per egg basis (Table 3). These results indicate that those pairs that produced the largest clutches were more successful in incubating those clutches and consequently produced more fledglings, not only in absolute terms but also in proportion to the size of their clutches.

Some recent theory would predict that reproductive success on a per egg basis would be equal among clutch sizes or would be negatively related to clutch size because both 1979 and 1980 were years of poor reproduction. For example, Högstedt (1980) proposed that clutch size is adjusted to the number of young that a pair can successfully rear to fledging and experimentally supported his hypothesis in an experimental field study using magpies (*Pica pica*). Boyce and Perrins (1987) proposed that reproductive success should be inversely related to clutch size in poor years, and Järvinen and Väisänen (1984) found that both hatching success and fledging success of Pied Flycatchers (*Ficedula hypoleuca*) were inversely related to clutch size in poor years. The positive relationship between clutch size and hatching success that we have documented contradicts the proposals of both Högstedt (1980) and Boyce and Perrins (1987) and suggests that those individuals producing relatively large clutches also were able to produce proportionally more hatched eggs from those clutches.

When we examined breeding performance in relation to location for the North Island 1980 sample, we found that initiation dates of clutches were comparable in both location types: both mean values and standard deviations were virtually identical (Table 4). Likewise, clutch size and the number of eggs hatching/clutch were equivalent. Nonetheless, the number of fledglings/clutch was significantly higher in areas with active nest sites in both years than in areas where active nest sites were present only in 1980 (Table 4).

We examined habitat attributes of nest sites in relation to location for the North Island 1980 sample. Habitat attributes of nest sites that were active in both years on North Island differed significantly from those that were active only in 1980 (Table 4). Nest sites used only in 1980 were in heavily vegetated areas dominated by *Heracleum*. Generally, nests in areas where nesting occurred in both years were at higher elevations and on gentler slopes than were those in areas where nesting occurred only in 1980.

In areas of active nesting in both years, nearest-neighbor distances averaged 2.9 m; nearest-neighbor distances were significantly greater, averaging 3.8 m, in areas that contained active nests only in 1980 (Table 4). Thus, territories were tightly packed in those areas where gulls initiated clutches in both years. We suggest that competition for territories was highest in the areas where clutches were initiated in both years. Such high-density nesting could adversely affect reproductive success (Hunt and Hunt 1976; Pierotti 1982, 1987). Ewald et al. (1980) found that killing of chicks was more prevalent on small territories than on large territories and that large territories were more heavily vegetated in a low-density colony of Western Gulls (*Larus occidentalis*). In contrast, we found in this study that nearest-neighbor distances and vegetative cover were lower and fledging success was higher on territories in areas used in both years than in areas where clutches were initiated only in 1980 (Table 4). Thus, differences in the quality (e.g., age or experience) or reproductive effort of breeding pairs apparently overrode the potentially adverse effects of high-density nesting in areas of comparatively low vegetative cover.

Incorporating clutch size, location code, and all habitat variables in a logistic regression analysis of nest success for the North Island 1980 sample showed that only clutch size and location code accounted significantly ($P < 0.05$) for variability in nest success. Both variables entered the stepwise model:

$$\text{Nest success} = \frac{\exp[-5.446 + 1.640\ (\text{clutch size}) - 0.949\ (\text{location code})]}{\{1 + \exp[-5.446 + 1.640\ (\text{clutch size}) - 0.949\ (\text{location code})]\}}$$

with $\chi^2 = 8.595$, 1 df, $P = 0.003$,

where the $\chi^2$ statistic is from a likelihood-ratio test of the model with clutch size and location code vs. the null model with just clutch size. This equation indicates significant relationships of both clutch size and location code to nest success. Statistically, the effects of clutch size and location code were independent ($\chi^2 = 0.90$, 2 df, $P > 0.20$). None of the 13 one-egg clutches and only four of the 62 two-egg clutches were successful. Among 181 three-egg clutches, the probability of nesting successfully was considerably higher in areas where nesting occurred in both years (38.1% of 84 attempts) than in areas where nesting occurred only in 1980 (18.6% of 97 attempts). As noted earlier, hatching success was positively and significantly related to clutch size (Table 3), and fledging success was related to location code (Table 4). Thus, the most successful nests in the North Island 1980 sample were in areas where nesting also occurred in 1979 and at nest sites where the pair produced a three-egg clutch.

Because no habitat variables entered the logistic model, the spatial differences in reproductive performance within the North Island 1980 sample suggest that there were persistent differences between years in the quality of adults that attempted to breed on Squab Island (see Coulson 1968). We did not individually mark adults; however, philopatry to particular areas probably is high (e.g., Vermeer 1963, Southern and Southern 1979). Pairs using some areas of the colony generally did not initiate nests in 1979 and had poor success during the chick period in 1980. Pairs in other areas generally initiated clutches and on average fledged one chick in 1979 and had significantly higher success during the chick period in 1980.

Our results suggest that pairs producing larger clutches either (1) were in better condition and were better able to maintain their condition while reproducing than were those who produced smaller clutches or (2) invested (risked) more during both egg-laying and incubation (Pugesek 1987). In 1979, food shortages were apparent from nest initiation through incubation, and it appears that those pairs that were able to accrue sufficient resources to produce the largest clutches also were best able to maintain their incubation schedules as adverse conditions continued. In 1980, those pairs that produced the largest clutches (when conditions were favorable) were best able to maintain their reproductive attempts late in the incubation period and during the chick period, when conditions were unfavorable (see Murphy et al. 1984). Thus, our results suggest that there was no trade-off between relative abilities of pairs to reproduce in favorable and unfavorable conditions; indeed, it appears that differences in quality that were expressed when conditions were favorable early in 1980 were amplified when conditions later deteriorated.

## ACKNOWLEDGMENTS

The project was funded by Contract No. CX-9000-8-0151 from the National Park Service to the Alaska Cooperative Park Studies Unit of the University of Alaska Fairbanks. The Institute of Marine Science, University of Alaska Fairbanks, provided equipment, facilities, ship time, and logistic assistance. We thank the Oldows, K. Knighten, and Harbor Air Service for their invaluable help in the field; F. C. Dean, J. W. Larson, and A. L. Lovaas provided support throughout the project and critically reviewed preliminary reports. T. A. Carpenter assisted in the field, and M. Snyder provided considerable logistical assistance. R. Pierotti and D. Siegel-Causey reviewed the first submittal, and R. T. Bowyer reviewed the revised manuscript.

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