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A COMPARISON OF NESTING-LEDGES USED BY SEABIRDS ON ST. GEORGE ISLAND[1]

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Abstract. Measurements of 288 nesting-ledges of six species of seabirds on St. George Island, Alaska, revealed significant interspecific differences in the size, shape, and overhang of ledges used. Typically, Red-legged Kittiwakes used ledges 1 dm deep; Northern Fulmars, Black-legged Kittiwakes, and Thick-billed Murres used ledges of an intermediate 2–4 dm depth; Red-faced Cormorants used ledges 3–6 dm deep; and Common Murres occurred singly on shallow ledges or in groups on deeper ledges. Fulmars and murres, which did not build nests, used nearly horizontal ledges exclusively; the nest-building species occurred on a wider range of slopes. Only the Red-legged Kittiwake regularly used ledges with over 50% cover by overhanging cliff within 5 dm of the ledge. Classification of the measured ledges of the cormorant, the two kittiwakes, and the Thick-billed Murre by a discriminant function analysis revealed significantly greater overlap than expected between the species pairs of cormorant with Thick-billed Murre, Black-legged with Red-legged Kittiwake, and Black-legged Kittiwake with Thick-billed Murre. Observations of 43 interspecific exchanges of nest sites during and between three breeding seasons agreed with the predictions by the discriminant analysis of overlap or lack thereof in three of four significant cases. Exchanges occurred significantly more frequently than expected between the species pairs of cormorant with Black-legged Kittiwake, cormorant with Thick-billed Murre, and Black-legged with Red-legged Kittiwake.

Key words: cliff nesting; colonial seabirds; discriminant function analysis; ledge nesting; nesting habitat; Phalacrocorax; *Pribilof Islands;* Rissa; *Uria.*

INTRODUCTION

Lack (1968:125) predicted that limited nesting sites may result in intense competition among nidicolous species of seabirds. Several authors give examples of potential competitive exclusion involving nesting sites of cliff-nesting seabirds (e.g., Uspenski 1956, Belopol'skii 1957, Stonehouse 1962, Kenyon and Phillips 1965, Smith 1966, Spring 1971, Maunder and Threlfall 1972, Williams 1974, Kepler 1978). Yet thus far, few (e.g., Smith 1966) have quantitatively documented differences in the nesting sites among species of cliff nesters.

We here describe quantitatively the nesting-ledges used by six species of seabirds on St. George Island, Pribilof Islands, Alaska. On the seacliffs of this island, Northern Fulmars (*Fulmarus glacialis*), Red-faced Cormorants (*Phalacrocorax urile*), Black-legged Kittiwakes (*Rissa tridactyla*), Red-legged Kittiwakes (*R. brevirostris*), Common Murres (*Uria aalge*), and Thick-billed Murres (*U. lomvia*) nest on ledges at extremely high density. To demonstrate interspecific differences among the ledges used, we compare the area, slope, and amount of overhanging cliff at each nest site. A discriminant function analysis allows us to evaluate interspecific overlap among the physical features of the nesting-ledges used. We compare the resulting predictions of overlap or lack thereof with observations of interspecific exchanges of nest sites during and between three breeding seasons, 1976–1978. Thereby, we address the hypothesis that physical overlap of nesting-ledges corresponds directly to interspecific competition for nest sites.

STUDY AREA

St. George Island (56°36'N, 169°32'W) lies in the southeast Bering Sea, 30 km north of the continental shelf edge. Seacliffs rising from 10 to over 300 m account for 49 km of its 58-km shoreline. The cliffs are often heavily fractured such that rock fragments may dislodge readily from many sections. On higher cliffs sheer rock faces are interrupted frequently by steep talus slopes covered by vegetation. Arctic foxes (*Alopex lagopus*) limit colonially nesting seabirds to inaccessible cliffs, offshore rocks, and holes among talus.

The ledges we sampled were on cliffs along the north side of the island between centrally located Staraya Artil and Tolstoi Point, the east end. Most cliffs in this area are <25 m except near Tolstoi Point where they rise to near 60 m. Even so, in this latter area, the ledges sampled were on lower buttresses that had faces seldom >20 m in height. In addition, we included in our sample 15 ledges of Common Murres located on an offshore rock 1 km southeast of Dalnoi Point, the west end.

METHODS AND DEFINITIONS

At the cliffs sampled, we measured all ledges which we could reach with a 9-m extension ladder. Only ledges containing nest sites at which an egg or chick

was present were measured. We measured the ledges of murres when eggs were present and those of fulmars, cormorants, and kittiwakes after chicks had hatched.

We defined a ledge as the uninterrupted surface, upon which the egg or nest rested, between the precipice of the cliff and the backwall. Protruding rock blocking the entire ledge constituted a boundary. The irregular nature of ledge boundaries and surfaces often forced us to decide boundaries subjectively within the context of this definition, and consequently, somewhat limited the precision of our measurements. We measured the following six variables over the entire surface of each ledge:

ledge-length = distance between ledge boundaries and parallel to cliff,

ledge-depth = distance from precipice to base of backwall measured perpendicularly to cliff,

ledge-slope = angle formed by the horizontal and the general slope of the ledge from the base of the backwall (we set horizontal equal to zero degrees; we recorded slopes toward the land in positive degrees),

backwall-slope = angle formed by a horizontal plane and the backwall (walls leaning over the ledge were recorded as <90° and those leaning away as >90°),

overhang-presence = the presence (1) or absence (0) of overhanging cliff within 5 dm above the center of the nest or above the egg,

overhang-coverage = proportion of the nest under overhanging cliff within 5 dm above the ledge, or for species that build no nest, the proportion of a circle of 1 dm radius from the egg site under such an overhang. (Note that a nest site may have an overhang present yet have an overhang-coverage <0.5 in cases of irregularly shaped overhangs.)

As part of a separate study on reproductive success (Hunt et al. 1981b), several sections of cliff containing nesting seabirds were selected for observation. These sections met three criteria: (1) a minimum number of nest sites present for at least one species; this minimum varied with the abundance of the species; (2) accessibility from the village within 1 h; (3) clear visibility from a safe overlook. There were 10 such sections on the north side of the island and three on the south side. On these cliffs we followed all nesting attempts, thereby obtaining records of interspecific exchanges of nest sites both within and between breeding seasons. Unfortunately, only a fraction of nest sites followed were accessible for measurement; furthermore, all ledges measured were not suitable for observation throughout the breeding season. There were no statistically significant differences in reproductive success for any species between these widely scattered sites (Hunt et al. 1981b). Therefore, we believe that the samples obtained in this study are representative of the colony as a whole.

RESULTS

During the breeding seasons of 1976, 1977, and 1978, we sampled a total of 288 ledges occupied by 468 nest sites of the six ledge-nesting species on St. George Island. The observed distributions of the variable overhang-coverage are obviously nonnormal; by definition, the variable is truncated at 0.0 and 1.0. The distributions are unimodal at 0.0 for all species except the Red-legged Kittiwake, for which it is bimodal at 0.0 and 1.0. Also, our data indicate that we may have rounded some observations of the variables overhang-coverage, ledge-slope, and backwall-slope to convenient values, e.g., 0.0 or 0.5, 0°, and 90°, respectively, when recording in the field. Nevertheless, our sample sizes are sufficiently large and the analyses sufficiently robust to use these data without transformation or grouping.

The nesting-ledge

Measurements of the defined variables show differences in the size, slope, and shape of contiguous cliff among nesting-ledges occupied by the different species (Table 1). One-way analyses of variance testing for equality of species means on a given variable are highly significant ($P < .005$, F, df = 3, 248) for the five variables ledge-length, ledge-depth, ledge-slope, backwall-slope, and overhang-coverage. Likewise, a chi-squared test for the variable overhang-presence is highly significant ($P < .001$, df = 5). We, therefore, reject the null hypothesis that no differences exist among nesting-ledges used by the different species.

The size of ledge used directly follows the size of the bird (Table 1) and, in the case of murres, its social nesting habits. Ledges >4 dm in depth were typically occupied by a pair of Red-faced Cormorants or by several pairs of Common Murres, although occasional members of both species nested on shallower ledges. Common Murres occurred on ledges as shallow as 1 and 2 dm, frequently sharing them with Thick-billed Murres. Red-legged Kittiwakes nested on the shallowest ledges, having a median depth of 1 dm. Most often Black-legged Kittiwakes and Thick-billed Murres nested on ledges of an intermediate 2–3 dm depth, and Northern Fulmars, on ledges of 3–4 dm depth.

Although most birds of all species chose to nest on nearly horizontal ledges, only the nest-building species occurred regularly on seaward-sloping ledges. Ful-

TABLE 1. Summary of measurements of nesting-ledges. Means and standard errors are presented by species for defined variables. RC = Red-faced Cormorant; NF = Northern Fulmar; BK = Black-legged Kittiwake; RK = Red-legged Kittiwake; CM = Common Murre; TM = Thick-billed Murre.

	Species					
Variable	RC	NF	BK	RK	CM	TM
Ledge-depth (dm)	4.0 ± 0.26	3.7 ± 0.33	2.1 ± 0.08	1.2 ± 0.05	6.0 ± 1.23	2.5 ± 0.15
Overhang-coverage (%)	14 ± 5.1	19 ± 8.6	21 ± 3.9	56 ± 4.3	0 ± 0.0	24 ± 3.5
Ledge-slope (°)*	−15 ± 2.3	−1 ± 0.9	−12 ± 2.0	−15 ± 2.1	−6 ± 2.7	−2 ± 0.5
Ledge-length (dm)	7.8 ± 0.42	7.8 ± 1.03	4.1 ± 0.26	2.7 ± 0.17	10.2 ± 2.95	5.3 ± 0.41
Overhang-presence (%)†	13	20	27	63	0	38
Backwall-slope (°)‡	86 ± 1.8	92 ± 4.3	89 ± 1.1	87 ± 1.1	97 ± 3.0	87 ± 1.2
Number of ledges	30	15	70	86	21	66
Nest sites per ledge	1.00	1.00	1.04	1.08	7.90	1.38
Mass of adults (g)§	1900	620	450	375	980	1080

* Slopes toward the land are >0.

† Overhang-presence is given as the proportion of ledges with an overhang.

‡ Backwalls leaning over the ledge are <90°.

§ From Hunt et al. 1981a.

mars and Thick-billed Murres, which build no nests, laid eggs exclusively on ledges with slopes of ≈10° or less from horizontal. Similarly, only 2 of 166 pairs of Common Murres laid eggs on ledges sloping >20° seaward from horizontal. In contrast, cormorants and kittiwakes are able to build nests on ledges with a wide range of slopes; the ledges under seven Red-legged Kittiwake nests sloped seaward 60° or more from horizontal. Still, more than three-quarters of the nest-building cormorants and kittiwakes occupied ledges sloping within 20° of horizontal.

The mean overhang-coverage of 56% for Red-legged Kittiwakes far exceeds that of any other species (Table 1); yet the distribution underlying this mean is strongly bimodal, with a third of the nests completely covered and another third with overhang-coverage of 20% or less. As measured by the variable overhang-presence, 63% of Red-legged Kittiwake nests were under overhangs; whereas, by this criterion only 38 and 27% of Thick-billed Murre and Black-legged Kittiwake nest sites, respectively, were under overhangs. For the latter two species, overhang-coverage of 40% or less accounted for over three-quarters of the sample. Overhangs occurred even less frequently over ledges of cormorants and fulmars; none of the Common Murre ledges sampled had overhangs. Thus, though many of its ledges lacked overhangs, only the Red-legged Kittiwake had a major proportion of nests completely covered by overhanging rock.

The ledges of Northern Fulmars differed from those of all other species in two respects. First, 7 of 15 ledges sampled were not of bare rock, which is the typical substrate for other species. Rather these fulmars laid on platforms composed of soil and rock fragments packed several centimetres above the bedrock. Second, fulmar ledges were often partially enclosed on the sides by protruding cliff; none of our defined variables measures this feature.

Although we have analyzed our data by each nest-

ing-ledge, we could have analyzed them by each nest site on a sampled ledge. This distinction is irrelevant when discussing the cormorant, fulmar, or kittiwakes, which infrequently had more than one nest site on a single ledge. However, several pairs of murres regularly used the same ledge (Table 1). Common Murres often nest in dense aggregations, several ranks deep on large ledges. In our sample of 21 ledges, the number of Common Murre nest sites ranged from 1 to 92 sites per ledge ($\bar{x}$ = 7.90 nest sites per ledge). Thick-billed Murres typically nest in single lines on long, narrow ledges or against the backwall of large ledges occupied mostly by Common Murres. In our sample, the largest number of Thick-billed Murre pairs per ledge was 6 ($\bar{x}$ = 1.38 nest sites per ledge). If we had analyzed our data by nest site instead of by ledge, we would have violated the statistical assumption of independence. However, our analysis of the data by ledge results in an underrepresentation of the size of ledge typically used by Common Murres because the single pair on a 2 × 3 dm ledge has the same influence on the mean as do the 92 pairs on a 15 × 65 dm ledge. Thus, for Common Murres the means of ledge-depth and ledge-length greatly increase to 12.3 and 41.1 dm, respectively, if nest sites are used to calculate the means. On St. George Island, most Common Murres nest on very large ledges.

Discrimination of the nesting-ledges of different species

We used a discriminant function analysis (Klecka 1975, Hull and Nie 1981) to evaluate our ability to differentiate nesting-ledges of different species. Our data for Northern Fulmars and Common Murres poorly represent the nesting habitat of these species for reasons mentioned above. Indeed, a discriminant analysis using all six species correctly classifies to species only 46% of the 288 ledges. Therefore, we included only the Red-faced Cormorant, the two kittiwake
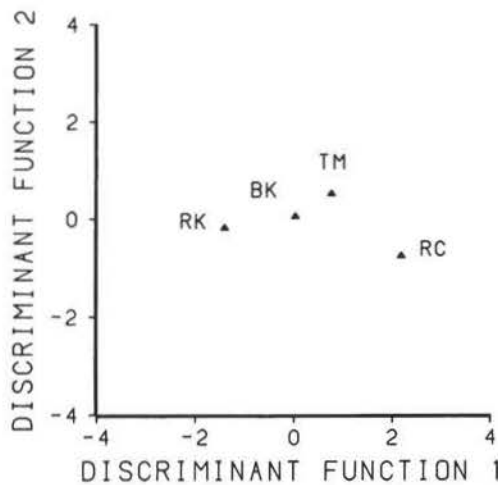
FIG. 1. Plot of species means for first two discriminant functions. Axes are in standard deviations. Function 1 accounts for 87% of the variance in the variables, whereas function 2 accounts for only 9%. Therefore, a given distance is more meaningful along the abscissa than along the ordinate. Abbreviations are as in Table 1.

species, and the Thick-billed Murre in subsequent analyses. These four species nest together in mixed colonies and use bare rock ledges, typically without enclosing sidewalls.

The discriminant analysis of these four species selected individual variables for inclusion in a stepwise fashion, using Rao's V as a criterion. Only the variables overhang-coverage and overhang-presence were highly correlated ($r = .84$); pairwise correlations were fairly low ($r \leq .33$) otherwise. The following four variables contributed significantly ($P < .05$) to the discriminating power of the analysis and were entered in the order: ledge-depth, overhang-coverage, ledge-slope, and ledge-length. The analysis used three discriminant functions, the maximum number allowable using four species; all three functions were significant ($P \leq .05$). The relative positions of the species mean values in a two-dimensional space created by the first two discriminant functions appear in Fig. 1. This relationship is almost one dimensional, as the first function accounts for 87% of the variation in the data. Ledge-depth was the most prominent variable in the first function, although all variables contributed substantially, as the standardized canonical coefficients in Table 2 demonstrate. Overhang-coverage and ledge-slope dominated the second function, which accounted for only 9% of the variance.

Using these discriminant functions the analysis then attempted to classify to species the 252 ledges. In the classification process, the individual species covariance matrices were used, and the prior probability of classification was equal for each species. The analysis correctly classified 65% of the ledges overall (Table 3).

Membership probabilities as indicators of habitat overlap

The above discriminant function analysis predicted for each ledge the probability of membership in each of the four species groups. The probability of membership in a species other than that of the actual occupant reflects the similarity of the ledges used by the two species. These probabilities should be higher between species using similar ledges than between those on dissimilar ledges (Table 3). We calculated standard normal (z) values from these probabilities for each pair of species. To do so we applied the formula:

(expected mean probability)

$$= \frac{[1 - (\text{mean probability for occupant species})]}{3}$$

to the mean probabilities in Table 3. We assumed that the probabilities of nonoccupant species were random occurrences. Then we summed the two z-values for each pair of species corresponding to the nondiagonal cells of Table 3. The left half of Table 4 contains the sign of the resulting z-values and their P-values. These z-values constitute a test of the null hypothesis that the probability of ledge membership in a nonoccupant species does not differ from that randomly expected for each pair of species. Rejection of this hypothesis combined with a positive z-value implies overlap in ledge habitat, as with the three pairs: Red-faced Cormorant with Thick-billed Murre, Black-legged with Red-legged Kittiwake, and Black-legged Kittiwake with Thick-billed Murre. A rejection combined with a negative z-value implies no overlap, as with the three pairs: Red-faced Cormorant with Black-legged Kittiwake, Red-faced Cormorant with Red-legged Kittiwake, and Red-legged Kittiwake with Thick-billed Murre.

Changes in occupant species as indicators of habitat overlap

We compared the above predictions derived from the discriminant analysis with our observations of interspecific changes at nest sites. The occurrence of nesting attempts by more than one species on the same ledge provides a biological indicator of species overlap on nesting-ledges. The numbers of nest sites followed

TABLE 2. Normally standardized canonical coefficients and percent of variance accounted for by each of the three discriminant functions.

	Discriminant function		
	1	2	3
Standardized coefficients			
Ledge-depth	0.754	−0.216	0.116
Overhang-coverage	−0.442	−1.006	0.874
Ledge-slope	0.394	0.735	0.404
Ledge-length	0.359	−0.127	0.295
Percent of variance	87.3	9.4	3.3

TABLE 3. Average probabilities of species of membership of 252 ledges from discriminant analysis.

Actual species	Number of ledges	Mean probability of species membership			
		RC	BK	RK	TM
Red-faced Cormorant (RC)	30	.64*	.12	.00	.24
Black-legged Kittiwake (BK)	70	.10	.46*	.17	.27
Red-legged Kittiwake (RK)	86	.02	.17	.69*	.12
Thick-billed Murre (TM)	66	.18	.25	.08	.49*

* Mean probability of correct classification.

during the 3 yr of study on St. George Island appear in Table 5. Excluding temporary changes in the species occupying a nest site, such as those involving loitering birds, we recorded 43 interspecific exchanges of nest sites within our study areas (Table 4). These include changes between breeding seasons and changes within one breeding season for which both species occupying the site had evinced ownership by defending the site, by nest building, or by egg laying. We standardized these data by comparing the observed frequency of nest sites exchanged between a pair of species with the frequency that would be expected if exchange were random.

Expected frequencies can be derived using the totals from Table 5 and population estimates from Sowls et al. (1978). Assuming random sorting, this expected frequency for species A and B, $E(AB)$, can be derived as

$$E(AB) = \frac{(Ab + aB)Y}{(1 - S)},$$

where A and B are the fractions of the given species of the total of all populations of interest on the island, a and b are the fractions of the given species of all nest sites under observation, Y is the number of interspecific exchanges observed, and S equals the sum of the products Aa, Bb, ... for all species of interest. The fraction $Y/(1 - S)$ accounts for intraspecific exchanges that we could not detect. If an expected fre-

quency is subtracted from that observed, the sign of the resulting difference indicates whether exchanges occurred more or less frequently than expected. These signs and P-values for chi-squared values with df = 1 derived from the observed and expected frequencies are given in the right half of Table. 4. The chi-squared values constitute a test of the null hypothesis that observed changes in species of occupant at nest sites do not differ from that expected if changes occur at random. As in similar tests above, a rejection of the hypothesis combined with a positive difference of observed and expected implies overlap, as in the pairs: Red-faced Cormorant with Black-legged Kittiwake, Red-faced Cormorant with Thick-billed Murre, and Black-legged with Red-legged Kittiwake. A rejection combined with a negative difference implies no overlap, as with the pair Red-legged Kittiwake with Thick-billed Murre.

Inspection of Table 4 reveals that there is agreement between the membership probabilities of the discriminant analysis and the observed exchanges of nest sites in three of four pairs of species. The remaining two pairs involved nonsignificant P-values for the observed exchanges.

DISCUSSION

The discriminant analysis revealed the most important variables to be ledge-depth, overhang-coverage, ledge-slope, and ledge-length. The biological impor-

TABLE 4. Membership probabilities of ledges from discriminant analysis and observed interspecific exchanges of nest sites as indicators of overlap.

Pair*	Ledge membership probabilities			Observed exchanges				Agreement?
	Sign†	P	Implies	Number of nest sites	Sign‡	P	Implies	
RC-BK	−	.000	No overlap	3	+	.000	Overlap	No
RC-RK	−	.000	No overlap	0	−	.429	NS§	⋯
RC-TM	+	.000	Overlap	10	+	.002	Overlap	Yes
BK-RK	+	.000	Overlap	20	+	.000	Overlap	Yes
BK-TM	+	.000	Overlap	9	−	.194	NS	⋯
RK-TM	−	.000	No overlap	1	−	.000	No overlap	Yes

* Abbreviations of names are as in Table 1.
† Sign of z value derived from sums of membership probabilities by species.
‡ Sign of observed value minus expected value derived from total observed exchanges and proportional population composition.
§ NS = not significant.

TABLE 5.　Number of individual nest sites, St. George Island.

	1976	1977	1978	Total nest-site-years
Red-faced Cormorant	11	27	68	106
Black-legged Kittiwake	34	110	229	373
Red-legged Kittiwake	88	240	235	563
Thick-billed Murre	40	92	125	257

tance of the variables concerned with the slope and size of a ledge is readily apparent. Across these variables, certain interspecific differences are clear (Table 1). That fulmars and Thick-billed Murres use nearly horizontal ledges almost exclusively is probably related to their non-nest-building habit. In cases of Common Murres using ledges sloping to 20 degrees seaward, the effect of the ledge slope may be offset by larger ledge depths. The nest-building Red-faced Cormorants and kittiwakes are less limited in the range of ledge slopes used.

The distinct differences observed in the size of ledge used certainly relate partly to differences in size (Table 1) and behavior of the species. Red-legged Kittiwakes use very small nesting-ledges, typically only 1 dm in depth, which would be of no use to the much larger Red-faced Cormorants. Yet the gregarious habits of the Common Murres, which occasionally use ledges as shallow as 2 dm, resulted in this species using some very broad ledges (Tuck 1960, Williams 1974) potentially to the exclusion of the much-larger cormorants. Nest structure also parallels ledge size. Stronger nests of more-adhesive materials are used on smaller ledges. Nests of Red-faced Cormorants on St. George Island are built mostly of vegetation and often do not survive intact until the end of the breeding season. The Black-legged Kittiwake uses more grass and less mud in nest building than does the Red-legged Kittiwake (Palmer 1899). Consequently, the foundations of the nests of Red-legged Kittiwakes commonly survive the winter to be built upon the following spring; in contrast, those of Black-legged Kittiwakes do so less frequently.

The biological significance of the remaining feature, rock overhangs, is not obvious. Rock overhangs occur commonly only above the ledges used by Red-legged Kittiwakes. Perhaps overhanging rock is desirable to this species, or perhaps it is simply the only species able to tolerate overhangs within 0.5 m of the ledge.

Our approaches to documenting interspecific overlap of the ledges used by seabirds on St. George Island are conceptually distinct. The first approach via the output probabilities of species membership by ledge from the discriminant analysis is based simply on the physical features of the ledge, as measured by our variables. These output probabilities may be influ-

enced by procedures of the discriminant classification process, by the limits of the information provided by our variables, and by actual interspecific overlap in the ledges used. We believe that these probabilities, which are significantly different from random, reflect actual overlap or lack thereof in the physical features of the ledges used by the four species in the analysis. The second approach, which used observed interspecific exchanges of nest sites, represents biological evidence of overlap through agreement in the selection of a specific nest site by members of different species. Unfortunately, our sample in the latter approach is small. Even so, that we observed a low rate of interspecific exchange among the four species, 0.03 (i.e., 43 exchanges in 1299 nest-site-years), certainly reflects the stability of the system.

The agreement between the two approaches is fairly good (Table 4). In the analyses, the Red-legged Kittiwake does not appear to overlap with either the Red-faced Cormorant or the Thick-billed Murre, as Fig. 1 implies. The lack of significance in exchanges between the cormorant and Red-legged Kittiwake very probably results from too small a sample. There is strong agreement for overlap between the cormorant and Thick-billed Murre and between the two kittiwake species. Kenyon and Phillips (1965) also noted conflicts at nest sites between the two kittiwakes on the Pribilofs. Though we observed significant overlap in physical features of the ledges used, the number of exchanges we observed between Black-legged Kittiwakes and Thick-billed Murres on St. George Island lay close to what would be expected from their relative populations if exchanges occurred at random. Competition for nest sites has been reported between these two species in other areas (Uspenski 1956, Belopol'skii 1957). There is disagreement in our analyses only for the pair Red-faced Cormorant with Black-legged Kittiwake.

The amount of agreement between the two approaches is especially noteworthy considering the differences in methods used. Again, the membership probabilities from the discriminant analysis are derived from data on the present distribution of certain physical characteristics of ledges among the species. In contrast, our observations of exchanges offer a more complete view of overlap, since all relevant criteria are certainly involved when birds select the nest sites. Thus, other factors must be considered in comparing the two approaches. For instance, an imbalance could exist in the nest sites available within a species' established range and its demand for nest sites. This point relates to the argument that the site that a species is using and what it is capable of using are not necessarily the same. Consider the discrepancy between the two approaches for the species pair Red-faced Cormorant with Black-legged Kittiwake. The larger cormorant cannot use ledges as small as those used by

the kittiwake; however, the opposite is not true. Also, we expect exchanges to occur at nest sites most similar to the established range of the participating species. For example, as Fig. 1 illustrates, in the space of the first two discriminant functions (ledge-depth, overhang-coverage, and ledge-slope), the typical Black-legged Kittiwake nest site lies about at the center of the means of the other species; in contrast, the typical Red-legged Kittiwake nest site is close only to that of its black-legged congener. Thus, if the Red-legged Kittiwake has a shortage of available nest sites, it has no place to go but to Black-legged Kittiwake sites. And last, biological factors such as the influence of the species on neighboring ledges (Coulson and White 1960, Klopfer and Hailman 1965, Nelson 1970, Coulson 1973) do not enter the first approach via membership probabilities yet are certainly operating in the second approach, via interspecific exchanges of nest sites.

Belopol'skii (1957) warns that any scheme of nest habitat partitioning derived from one locale should not be accepted implicitly, since the species may change habitat preferences as conditions change. Several references exist to the range of nest sites used by the Common and Thick-billed Murres (Belopol'skii 1957, Tuck 1960, Spring 1971, Williams 1974). On Bear Island where the two murre species breed, Common Murres are restricted to large flat areas; whereas, farther south in Europe where only the Common Murre breeds, it uses both large flat areas and cliff ledges (Lack 1968, Williams 1974). Lack (1968) considers this situation an example of competitive exclusion. The Thick-billed Murre, too, may change its range of nest sites to include large, open ledges, as Uspenski (1956) noted Thick-billed Murres breeding on ledges tens of metres across.

In summary, our statistical analyses show that the characteristics of nest sites vary between species of cliff-nesting birds. The site features of principal importance are ledge-depth, overhang-coverage, and ledge-slope. This separation of site-types agrees well with the subjective impression that the various seabird species have partitioned nest site types, with a concomitant reduction in interspecific competition. However, the observation of nest site exchanges between species, while generally in concordance with the relative distances found in the discriminant analysis, demonstrates that ecological segregation of these species is not sufficient to prevent interspecific competition. This finding illustrates the importance, when measuring niche overlap and resource partitioning, of examining direct interactions between the species involved, in addition to measuring physical aspects of the resource in question.

ACKNOWLEDGMENTS

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