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NEST SITE SELECTION BY KELP GULLS IN SOUTHERN AFRICA

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ABSTRACT.—We studied six colonies of Kelp Gulls (*Larus dominicanus*) in South Africa and Namibia, including mainland beach and cliff, and island sites. In the 20 distinct habitats examined, the gulls generally nested in somewhat horizontal areas with either intermediate vegetation cover (25 to 50%) or protruding rocks which provided similar cover. Characteristics favored for nesting were studied by comparing nest sites with matched points 2 m away. In all habitats the gulls selected flatter areas (mean slope less than 15°) than the matched points (mean slopes up to 70°). Selection of nest sites with more cover may serve to reduce chick loss by providing shelter (vegetation or rock crevices), and the gulls' choice of low rather than tall vegetation may ensure that adults can escape rapidly from the nest.

Colonial birds select their habitat and nest sites according to environmental and social factors. For many species, the process of nest site selection involves: 1) habitat selection, 2) choosing a part of this habitat on the basis of particular physical factors (such as elevation, slope, rocks, vegetation), 3) defining territorial boundaries as a result of contacts with neighbors (not necessarily conspecifics), and 4) selecting the nest site. Habitat selection, the choice of a type of place in which to live, results in animals living in a restricted set of environmental conditions (Partridge 1978). Once a habitat is chosen, birds either select a nest site and then negotiate territorial boundaries with neighbors, or they may defend a territory possessing the general features required, and subsequently select the nest site in that territory. In a few species of gulls, territories and nest sites are acquired simultaneously. For example, Franklin's Gulls (*Larus pipixcan*) in the United States and Brown-hooded Gulls (*L. maculipennis*) in Argentina defend territories from a mat of floating vegetation which later becomes the nest site (Burger 1974a, b).

In other gull species, territories are defended for weeks or months prior to nest building (Tinbergen 1956, Bongiorno 1970), and the territorial boundaries are fixed before the nest site is selected. These birds have elaborate behaviors for choosing the nest site, several locations being examined and many scrapes made before the final site is chosen (Tinbergen 1956, Bongiorno 1970). Gulls that select nest sites after acquiring territories must choose from the physical features available in those territories. Assuming, for example, that medium cover (ca. 50%) is preferred and that vegetation cover varies throughout the colony, gulls who choose 30% cover in sparsely vegetated areas or 70% cover in densely vegetated areas might be selecting the best cover available in their particular territories.

General nest site requirements of gulls have been examined in some detail, particularly in marsh-nesting species (Bongiorno 1970, Montevecchi 1978, Burger and Shisler 1978). The factors influencing colony and nest site selection in dry land colonies of gulls or terns have not been studied as extensively. Blokpoel et al. (1978) compared plots with and without nesting Common Terns (*Sterna hirundo*), and reported a preference for vegetated versus bare areas. Veen (1977) reported that Sandwich Terns (*S. sandvicensis*) exhibit rather uniform choices for nest sites with respect to vegetation and substrate, but he did not quantify these variables or compare nests with random points. Moreover, most investigators have worked in only one colony making generalizations for a species tenuous.

Several studies on nest site selection in gulls have compared the features of nest sites with those of random points distributed through the entire colony (e.g., Montevecchi 1978, Burger and Shisler 1978). The comparisons indicate general preferences for particular habitat characteristics, but do not indicate how birds choose a particular nest site among the numerous potential sites within their territories. Site selection

TABLE 1. Characteristics of major habitats in Kelp Gull colonies.

		Vegetation			Rocks[b]	
Colony	Habitat	Growth form[a]	Mean height (cm)	Percent cover	Type	Percent
Marcus	All nests	A,B,C	70	10	1,2,3	90
Malagas	All nests	E	40	10	1,2,3,4	90
Swakopmund	Rock	0	0	0	3	20
	Sand-rock	0	0	0	3	5
	Sand	0	0	0	3	2
Swartklip	Top	A,F,E	40	60	3,4	40
	Sand/rock cliff	C	30	12	3	5
	Sand cliffs	C	30	5	0	0
Die Mond	Bushes	A	125	75	0	0
	Herb	D	45	40	0	0
	Sand dunes	C	75	18	0	0
Schaapen	Cliff—D	0	0	0	1,2,3	100
	Beach—F	0	0	0	0	0[c]
	Open sand–B	B	70	2	3	2
	Sparse sand—C	D	40	25	3	4
	Small rocks—G	E	20	40	2	40
	Emergent rocks—E	D,F	40	20	1,2,3	80
	Flat rock—A	F	10	5	3,4	95
	Central—H	E,F	10	45	3	20
	Mint—I	B	75	62	0	0

[a] Refer to Figure 1 for diagram of growth form.
[b] 1 = large (up to 2 m tall); 2 = intermediate, 3 = small (less than 10 cm tall) and 4 = flat.
[c] The rest of the area is sand and gravel.

is constrained by the features available within a pair's territory rather than by the spectrum of features available in the colony as a whole. Comparisons of nests with matched points placed at some distance from the nest, but within the same territory, provide a means for evaluating how birds may choose nest sites. This technique has been used in studying nest site characteristics of Black Skimmers (*Rynchops nigra*; Gochfeld 1978).

In this paper we examine nest site selection in six Kelp Gull (*L. dominicanus*) colonies in southern Africa, in several habitats ranging from sandy islands to cliffs. We investigated how gulls might select nest sites with respect to the physical features within their territories, and compared these apparent choices among habitats and colonies. Over a wide range of colony sites which had probably been chosen many years earlier due to their protection from intrusions, we assumed that these gulls would have basically similar requirements with regard to physiognomy (e.g., slope, substrate, cover). Hence, we predicted that they would select characteristics which were more similar among the colonies than the average of characteristics available in these colonies.

Kelp Gulls nest in South Africa, South America, New Zealand, Australia, the Antarctic and subantarctic islands, and Madagascar (Moynihan 1959, Fordham 1964, Watson 1975, Brooke and Cooper 1979). No other gull nests along the coast of South Africa during the summer months (McLachlan and Liversedge 1978), suggesting that colony and nest site selection is not restricted by congeneric competition as it is in most other regions where gulls breed. Little has been reported about the habits of Kelp Gulls except for Fordham's (1963, 1964) study of their breeding biology in New Zealand, and Siegfried's (1977) description of mussel-dropping behavior in South Africa. Fordham (1964) described a variety of nest sites including bare sand or rock, herbaceous plants and bushes.

METHODS

STUDY SITES

During the 1979–1980 breeding season we examined five Kelp Gull colonies in the Cape Province, South Africa, and one colony in Namibia (South West Africa). Our visits to colonies were brief, allowing sufficient time to obtain measurements on habitat and nest site characteristics. The Die Mond colony (2.1 ha) is located 23 km SE of Bredasdorp (20°10'E, 34°44'S) on a beach fronting the Indian Ocean. The colony, containing 282 nests at the time of our visit, is in a flat vegetated basin between 20-m high barren sand dunes, and is isolated by barren sand flats hundreds of meters wide. We divided the colony into three major habitats on the basis of type and percent cover of vegetation. Gulls nested mainly in bare sand and at the edge of bushes rather than in the mixed vegetation. Table 1 summarizes the main characteristics of each habitat.

The Swartklip colony (2.1 ha), on the mainland 26 km SE of Cape Town (18°46′E, 34°05′S), contained about 200 pairs of Kelp Gulls nesting on the top and slopes of sandy and rocky cliffs overlooking the Atlantic Ocean. Gulls nested mainly on the heavily vegetated rock ledges, mostly at the top of the cliffs.

The three other South African colonies are located on rocky islands in Saldanha Bay about 95 to 110 km NNW of Cape Town (18°E, 33°S). Malagas Island (9 ha) contained nine pairs of gulls nesting together on the edge of a colony of Cape Gannets (*Morus capensis*). Marcus Island (11 ha), connected by a causeway to the mainland, contained 52 pairs of Kelp Gulls nesting among rocks and vegetation. No discrete habitats were distinguished on these islands. Schaapen Island (41 ha), in the sheltered portion of the bay, contained more than 3,000 pairs of nesting gulls. We divided it into nine distinct habitats ranging from sandy beaches to rocky cliffs. Gulls nested mainly in flat rocky places and avoided extremes such as the sandy beach and the rocky cliffs.

At Swakopmund, Namibia (14°07′E, 23°02′S) we found 134 gull nests on a sand and gravel island in a salt lake. Two other small islands nearby also contained nesting Kelp Gulls. Gulls nested mainly near the protruding rocks in the center of the small (0.5 ha) island.

All colonies in South Africa were at a comparable stage of the breeding cycle (i.e., about 60% of the nests had chicks, and about 80% of chicks were less than 10 days of age). The Swakopmund gulls, however, were mainly in early incubation. The Swartklip colony is shown on some local maps as Wolfgat. The Afrikaans name of Schaapen Island is equivalent to the English name, Sculpin Island, and both names have appeared in the literature.

PROCEDURES

In four colonies (excluding Malagas and Marcus) we distinguished distinct habitats according to physiognomic characteristics (see Table 1, Fig. 1). After describing the general habitat types in each colony we selected at random 20 nests in each habitat, and for each nest we located a matched point 2 m from the nest center in a randomly chosen direction (one of the 16 compass points). This distance was selected a priori because it is close enough to be within a Kelp Gull's territory (Fordham 1963, 1964), yet far enough away to be outside of a plant or rock immediately adjacent to the nest. In most habitats there was little correlation between characteristics at nests and matched points, thereby validating this choice of distance. Significant positive correlations would occur if the distance were too small. Some significant correlations are expected in any case (Table 3), since nest site characteristics are related to habitat characteristics.

At the nest sites and matched points we recorded the following data: percent vegetation cover and rock cover within 1 m of nest, distance to nearest protruding rock, distance to nearest vegetation, distance to nearest plant of the dominant species, and height of the dominant vegetation. At the Die Mond colony, where the substrate was undulating, we recorded whether the nest and the matched point were on the crest, slope, or in a trough. For all nests and matched points, we measured the slope averaged over a 30-cm distance centered at the nest center or point.

To test apparent preferences we compared the characteristics of nest site and its matched point within habitats using sign tests (Siegel 1956), rather than comparing means for each sample. In some cases with nonsignificant sign tests, we found strong bimodal distributions of matched points, and used contingency table analysis with chi square tests.

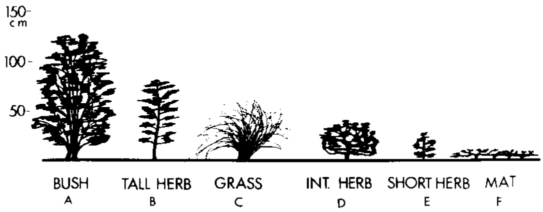

FIGURE 1. Schematic representation of growth forms of plants discussed in this paper. Letters correspond to entries in Table 1.

Assuming that steep slope and either excessive or inadequate cover would jeopardize a nest or chicks, we predicted that gull nests would be on more level sites and closer to rocks or vegetation than the matched points. Moreover, we predicted that in sparsely vegetated habitats gull nests would be in heavier cover than the matched points and vice versa in very dense habitats. Thus we anticipated that, particularly with respect to cover, nest sites would show less inter-habitat variation within colonies than the corresponding matched points. Our predictions led us to use one-tailed tests of significance. We performed one-way analysis of variance on log-transformed data for distances, using separate analyses for matched points and nests within each colony. We then made direct comparisons of the F-values to determine whether nests or matched points showed greater habitat-related variability.

RESULTS

Three types of environmental characteristics varying among and within Kelp Gull colonies were studied in detail.

SLOPE

The sites used by nesting Kelp Gulls ranged from horizontal surfaces to ledges on nearly vertical cliffs of sand or rock. Some colonies (e.g., Swartklip, Schaapen) offered the full range of slope conditions, while others were primarily flat. In all colonies, and in all habitats (except the sparse sand on Schaapen), gulls chose nest sites which were significantly more level than the matched points (Figs. 2, 3, 4). Table 2 gives statistical comparisons of nests and matched points. For most habitats there was no correlation for slope between nests and matched points (Table 3). At Die Mond the significant correlation in the mixed herb habitat can be accounted for in part by the gulls' nesting on mounds of sand. We therefore examined the gulls' apparent choice of nest site in more detail. Due to the undulating substrate, each nest or point could be characterized as crest, slope or trough. Using 2 × 2 contingency tables, we found significantly more nests on crests (versus non-crest) in the dune ($\chi^2 = 7.10$, $P < 0.01$) and mixed herbs ($\chi^2 = 6.10$, $P < 0.02$), but no difference in the bush habitat.

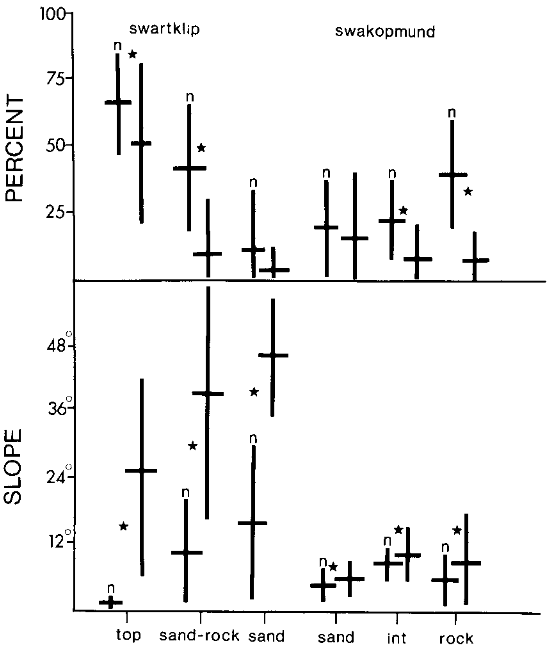

FIGURE 2. Mean percent cover (upper) and mean slope in degrees (lower) for nests (n) and matched points by habitats in Swartklip and Swakopmund Kelp Gull colonies. Mean (horizontal bar) and SD (vertical line) are shown. An asterisk indicates significant difference ($P < .05$) by Sign Test.

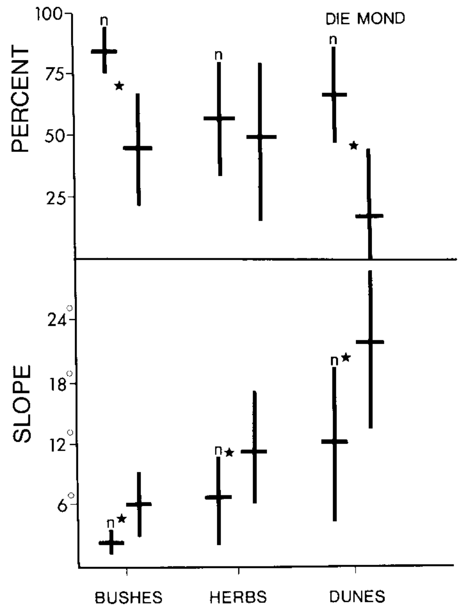

FIGURE 3. Mean percent cover (upper) and mean slope in degrees (lower) for nests (n) and matched points by habitats in the Die Mond Kelp Gull colony. Mean (horizontal bar) and SD (vertical line) are shown. An asterisk indicates significant difference ($P < .05$) by Sign Test.

In comparing the slopes for nests with matched points, we found that in all habitats the mean slope for nests was less than 15° while mean values for matched points ranged up to 70° (Fig. 5). The overall rank correlation for slope among habitats was positive (Kendall tau = 0.43, $P < 0.01$), indicating that choice of nest site was limited by the available sites as estimated by the single matched points.

If the gulls were selecting a narrow range of nest site characteristics from a wider range of possibilities, variability among habitats should have contributed more significantly to variation among matched points than to variation among nests. The comparison of the F values from the one-way ANOVA did reveal higher F values for the matched points for slope in all colonies.

VEGETATION

Several characteristics of vegetation could affect choice of nest sites: percentage of cover, species, growth form, and height of plants. In areas of low cover, nest sites generally had more cover than matched points (Figs. 2, 3, 4). Only at Schaapen did the gulls choose nest sites with significantly less cover than the matched points (Fig. 4). On Marcus Island, the percentage of vegetation cover around nests (mean ± SD, 25 ± 24%) did not differ significantly from the matched points (34 ± 40%; Table 2). Only in the mixed herb habitat at Die Mond was there a positive correlation for cover between nests and matched points; large patches of vegetation (5 to 10 m across) formed a mosaic. Comparing F-values from ANOVA we found that only at Die Mond and Swartklip, where in some habitats gulls nested mainly next to rocks rather than plants, was there higher variation in percent cover around nests than around matched points.

In most habitats the gulls did not appear to select particular plant species (Table 2). We determined whether gulls nested closer to the dominant vegetation, and whether they nested closer to any vegetation, compared with their matched points. For example, at Schaapen no overall pattern emerged with respect to the type of vegetation (Tables 2, 4), although there was a pattern with respect to distance to vegetation. In habitats where rocks did not provide crevices for cover (i.e., small rock, mint, central, and cliff habitats), gull nests were closer to vegetation than were the matched points. In habitats with little vegetation (i.e., open sand and sparse sand), the gulls were unable to nest close to cover.

We predicted that since the physiognomy of the dominant vegetation might influence

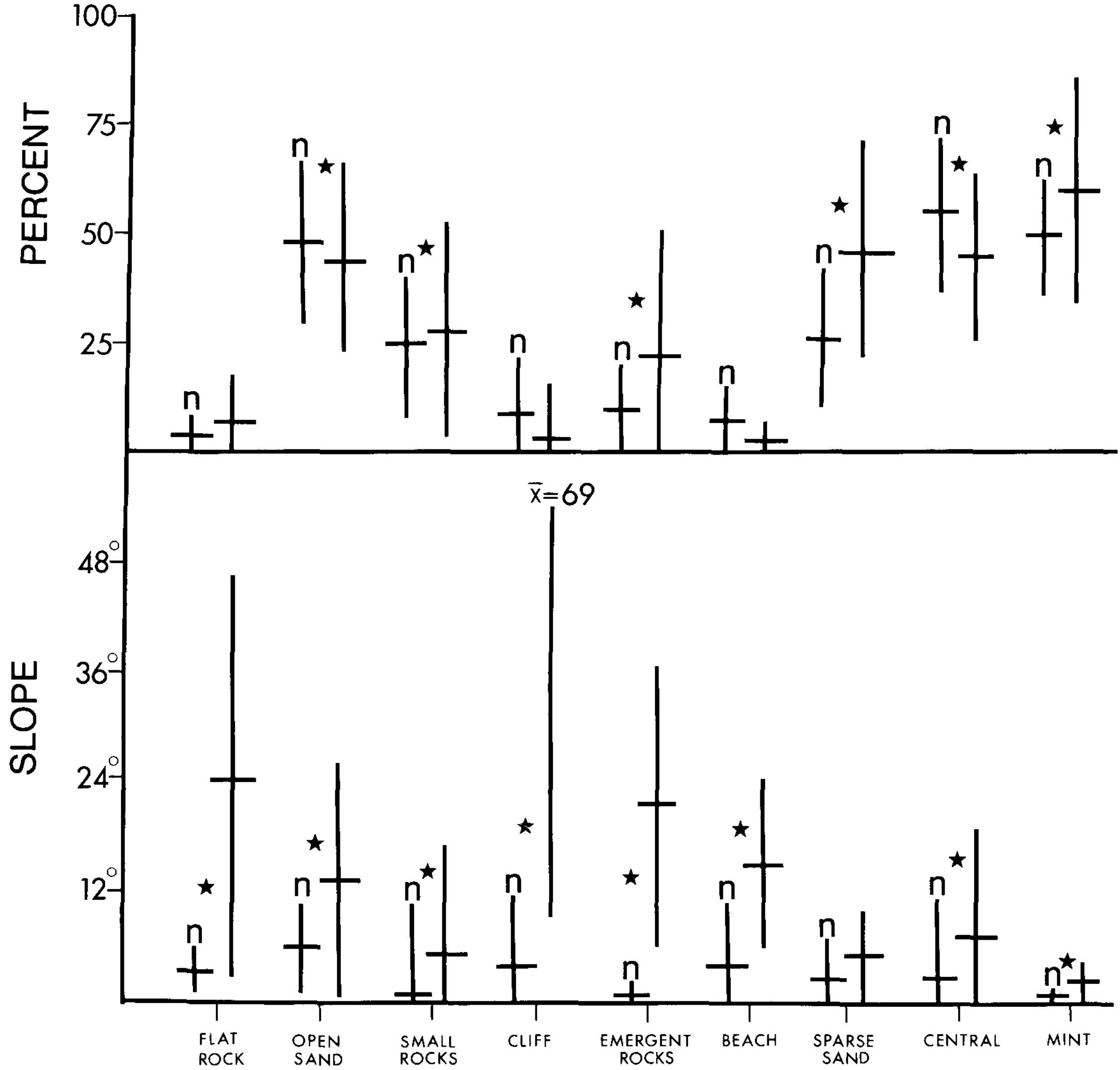

FIGURE 4. Mean percent cover (upper) and mean slope in degrees (lower) for nests (n) and matched points by habitats in the Schaapen Island Kelp Gull colony. Mean (horizontal bar) and SD (vertical line) are shown. An asterisk indicates significant difference ($P < .05$) by Sign Test.

habitat choice, gull nests would be closer to the dominant vegetation than would the matched points. However, this was not the case in five of the eight habitats on Schaapen. Only in habitats where rocks were absent or sparse (i.e., central and mint habitats), were nests significantly closer to dominant vegetation compared to the matched point. Similarly at Die Mond, in the bush and herb habitats mean distances to vegetation were not significantly different for the nests (1.6 ± 2.1 cm) and matched points (5.2 ± 8.0 cm), whereas in the dunes the nests were closer (3.1 ± 8.1 cm) than the points (24 ± 31 cm; Table 2). However, with respect to dominant vegetation, the nests in the bush habitat were closer to bushes. In fact, the nests were often immediately adjacent to or under bushes, resulting in a distance of 2.2 ± 5.0 cm, compared to the matched points (45 ± 44 cm). At Die Mond it was only in the dune habitat that there was a correlation for distance to vegetation between the nests and the matched points (Table 3).

Vegetation height also influenced the gulls' choice of nest sites. For example, at Swartklip on the top and on the rock-sand cliffs, nest sites had taller vegetation than did the matched points. On the top ledge, vegetation height near nests averaged 24 ± 17 cm, compared to 17 ± 21 cm for the matched points (Sign Test, $P < 0.04$).

ROCKS

Rocks varied from flat level surfaces to jagged vertical surfaces. Rocks could influence nest site selection with respect to substrate

TABLE 2. Comparison of nests and matched points. Given are *P* values from a Sign Test. An asterisk indicates that a chi-square goodness of fit test was used.

				Distance from nest to		
Colony	Habitat	Percent cover	Slope	Any vegetation	Rocks	Bushes
Die Mond	Bush	.01	.006	.25	—	.02
	Mixed herb	.40	.001	.10	—	.001
	Dunes	.001	.032	.001	—	—
Swartklip	Top ledges	.40	.001	.20	—	.20
	Sand-rock-cliff	.001	.001	.20	—	.20
	Sand cliffs	*.23	.001	.20	—	.20
Marcus	All nests	*.50	*.015	.30	*.002	—
Schaapen	Flat rock	*.50	.006	*.13	*.01	—
	Open sand	*.05	.001	.40	*.05	—
	Small rocks	*.001	.002	.05	.006	—
	Cliff	.09	.001	.02	*.001	—
	Emergent rocks	*.05	.001	*.25	.006	—
	Sparse sand	*.001	.20	.05	.30	—
	Central	*.01	.001	*.05	.30	—
	Mint	.05	.001	.05	.40	—
Swakopmund	Sand	.30[a]	.05	—	.30	.30[b]
	Sand-rock	.001[a]	.05	—	.30	.40[b]
	Rock	.001[a]	.05	—	.005	.02[b]

[a] Percent cover refers to rock cover, not vegetation cover.
[b] Distance to water's edge.

and to the cover they provided. On Schaapen, rocks provided the main cover in several habitats, and in all habitats nests were closer to rocks than were the matched points (Tables 2, 4). In these habitats (flat rock, open sand, small rocks, cliff, emergent rocks) the gulls nested within 10 cm of rocks, whereas the matched points averaged 20 to 221 cm to rocks. Similarly the nests on Marcus Island were closer to rocks (23 ± 52 cm) than were the matched points (52 ± 40 cm; Table 2). On Malagas Island, where the substrate was entirely rock, nests were closer to upright rocks than were matched

TABLE 3. Correlations for several characteristics between nests and their matched points in Kelp Gull colonies. * = $P < 0.05$, ** = $P < 0.01$.

				Distance to		
Colony	Habitat	Percent cover	Slope	Any vegetation	Dominant vegetation	Rock
Schaapen	Flat rocks	+.007	−.206	+.749**	+.729**	−.125
	Open sand	+.051	+.200	+.931**	+.480*	+.983**
	Small rocks	+.029	−.128	+.301	+.571**	+.607**
	Cliffs	+.260	+.120	+.928**		−.155
	Emergent rocks	−.201	−.074	+.566**	−.164	+.096
	Sand beach	+.415	+.351	+.979**	+.981**	−.064
	Sparse sand	−.057	−.112	−.032	+.622**	+.901**
	Central	.0	+.125	+.001	+.033	+.961**
	Mint	+.216	−.028	−.087	+.032	
Swartklip	Top ledges	+.235	−.248			
	Sand-rock-cliff	+.405	+.355			
	Sand cliffs	+.194	+.253			
Swakopmund	Sand	−.203[a]	+.263			.545*
	Sand-rock	−.012[a]	+.449*			.742*
	Rock	+.380[a]	+.126			.095
Die Mond	Bush area	−.030	+.359	−.20	−.150	
	Mixed herbs	+.561**	+.616**	+.111	+.607**	
	Dunes	+.213	+.366	+.788**	+.493*	
Marcus	All nests	−.312	+.291	−.112		+.189

[a] Cover refers to rock rather than vegetation.

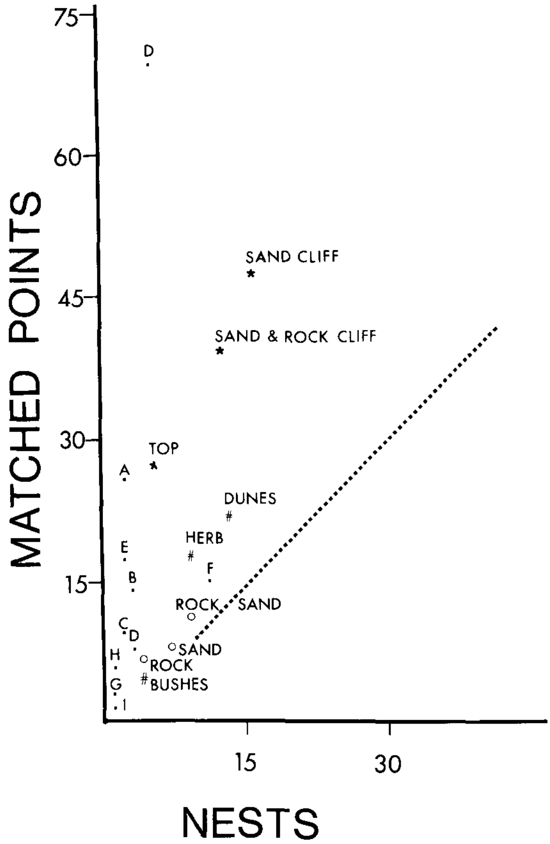

FIGURE 5. Mean slope of matched points plotted against mean slope at nests for all habitats in all colonies. The diagonal line signifies equivalent slope for a nest and its matched point. Letters refer to habitats on Schaapen Island (see Table 1 for code). Symbols refer to colonies as follows: · = Schaapen, * = Swartklip, # = Die Mond; o = Swakopmund.

points (χ^2 = 13.3, $P < 0.01$). Using the F values from ANOVA we found that in Schaapen and Swakopmund there was no significantly greater inter-habitat variation influencing matched points than nests.

SUBSTRATE

In most colonies, the ground was nearly uniform (e.g., Die Mond, Swakopmund, Malagas). Certain colonies, however, had both dense mats of vegetation and flat level rocks, offering nesting gulls a choice of substrate. In most habitats on Schaapen Island gulls nested on rocks, sand, or vegetation. We tested their apparent preferences for substrate in each habitat using contingency tables. In the flat rock habitat almost all gulls nested on sand whereas the matched points were usually on rock (χ^2 = 6.66, P <0.03). In the sparse sand (sparsely vegetated sandy area), gulls nested only on sand, while matched points often fell on vegetation (χ^2 = 14.5, $P < 0.01$). In the emergent rock habitat, however, gulls nested mainly on rock while matched points were sometimes on sand or vegetation (χ^2 = 5.99, P <0.05). There was no difference in the other habitats. Summing across all habitats, gull nests were significantly more frequent on sand than on rock or vegetation (χ^2 = 14.6, $P < 0.001$). The different result in the emergent rock habitat suggests that substrate is of secondary importance in determining nest site. Similarly on Marcus Is-

TABLE 4. Distances (in cm) to any vegetation, to dominant vegetation and to rocks, of nests and matched points on Schaapen Island. * = $P < .05$ comparing nests with matched points, using Sign Test.

		To closest vegetation	To dominant vegetation	To rock
Flat rock	Nests	235.4 ± 211	166.4 ± 202	*3.9 ± 7
	Matched points	208.4 ± 195	185.6 ± 156	36.4 ± 47
Sand beach	Nests	565.7 ± 528	188.1 ± 204	*8.1 ± 13
	Matched points	582.8 ± 502.7	310.9 ± 309	62 ± 88
Open sand	Nests	197.3 ± 318	6.3 ± 8	*211.5 ± 485
	Matched points	177.6 ± 277	15.4 ± 36	221.6 ± 458
Sparse sand	Nests	*3.1 ± 3	19.6 ± 31	469.6 ± 407
	Matched points	14.4 ± 9.9	19.2 ± 26	493.0 ± 385
Small rocks	Nests	*51.4 ± 85	27.1 ± 53	*43.4 ± 86
	Matched points	50.3 ± 51	33.5 ± 38	33.9 ± 78
Emergent rocks	Nests	229.0 ± 156	39.3 ± 52	*1.7 ± 4
	Matched points	180.1 ± 121	24.9 ± 1.6	20.9 ± 25
Central	Nests	*0.9 ± 2	*26.1 ± 50	613.3 ± 468
	Matched points	14.8 ± 32	39.4 ± 34	647.5 ± 472
Mint	Nests	*1.4 ± 2	*3.2 ± 6	none
	Matched points	42.3 ± 60	7.3 ± 16	

land gulls nested mainly on sand while matched points were mainly on rock ($\chi^2 = 17.4$, $P < 0.001$).

DISCUSSION

In this study we found Kelp Gulls nesting on sites which were mostly free from mammalian predators (i.e., islands), difficult for mammalian predators to negotiate easily (rock and sand cliffs), or isolated by stretches of barren sand (i.e., sand dune colony at Die Mond). Avian predators such as conspecifics and Eastern White Pelicans (*Pelecanus onocrotalus*), did have access to the colonies. Within these colonies Kelp Gulls avoided the most open areas with little cover, steep rock or sand slopes, and dense or tall vegetation. They nested wherever rocks or vegetation provided moderate cover in flat areas. The above considerations relate to colony and habitat selection. Once a pair of gulls has selected a territory on the basis of physical conditions in the colony, they select their nest site according to a subset of characters available within their territory. Our comparison of nest sites and matched points provides an a posteriori means of determining the basis for nest site selection.

MATCHED POINT METHOD

Matched points located at a fixed distance and random direction from a nest provide a means of comparing the characteristics of the nest site with characteristics available elsewhere in the same territory. The choice of a 2-m distance was based partly on information on territory size provided by Fordham (1963, 1964), and was tested empirically in the first colony we visited (Swartklip). The choice of distance for placing the matched point depends on the territory size (or density) and on the texture or patch size of the environment; the problem is the same as the selection of appropriate quadrat size for ecological sampling.

An optimum distance exists for each habitat and density condition, and this can be determined by using several matched points at different distances in each territory (Gochfeld, unpubl. data). However, for a comparison of the sort provided here, a single distance is desirable whenever possible. Correlation analysis can be used to determine whether the distance chosen is too small. If most correlations are significantly positive, a larger distance is necessary. If most comparisons show no correlation between nest and matched point, the distance is not too small. If gulls nested in the center of their territory, then a distance equal to one-fourth of the distance to their nearest neighbor might prove desirable for sampling. Frequently, however, they do not nest at the center. The results presented in Table 3 indicate that relatively few comparisons (22 of 74) were positive, thereby validating our choice of a 2-m distance from a nest to a matched point. The distance is more suitable for comparisons of percent cover and slope (its original purpose) than for comparing distance to vegetation. Thus if a territory was in an area with no vegetation, both the nest and the matched point would be far from vegetation, and a distance much larger than 2 m would not have affected the result.

NEST SITE CHARACTERISTICS

Kelp Gulls apparently chose nest sites within their territories on the basis of slope and cover. In all cases they nested on the most level sites available. This choice is probably adaptive since eggs and chicks are less likely to roll or fall from level nests. On the steep slopes of Swartklip, for example, we found many nests that had slipped downslope when supporting rocks or vegetation had given way. We compared the mean brood size on the top and on the sides of the cliffs ($\chi^2 = 13.3$, $P < 0.01$, based on unpublished data), and found that many nests on the slopes had lost eggs or chicks.

The second habitat feature that appeared consistently important was cover. Both rocks and vegetation provided cover, and gulls nested next to one or the other, but not necessarily both. At Schaapen, gulls nested next to rocks in emergent rock, open sand, flat rock, small rock, and cliff habitats, while they nested next to vegetation in other habitats. Where both vegetation and rocks were present they seemed to prefer rocks. Both rocks and vegetation could provide some shade from the sun, protection from wind and rain, and concealment from avian predators. Rocks have added advantages of being cooler than sand in the hot sun and retaining heat longer after sunset. Moreover, unlike bushes, rocks do not seem to impede adults that have been frightened from the nest (unpubl. observ.). Since vegetation grows during the nesting cycle, it would provide more and taller cover for chicks than when the nest sites were originally chosen. Conversely, the physical features of rocks do not change during the breeding season.

Gull nests in most habitats (particularly those with sparse vegetation), had more vegetation than the corresponding matched point. The exceptions occurred where plants were uniformly distributed (e.g., open sand and mint habitats on Schaapen). Thus in most habitats nest sites had minimum slope and maximum rock or vegetation cover, although areas with cover exceeding 70% were generally avoided entirely. We were surprised to find that the type of vegetation was less important than cover, and that after choosing a habitat, birds apparently might ignore the dominant vegetation there.

We have documented that Kelp Gulls nest in various habitats, differing in substrate and cover. Our findings support Fordham (1964), who found these gulls nesting in habitats ranging from unsheltered cliff ledges to heavily vegetated bushy areas. The range of nest sites used in New Zealand seems similar to that in southern Africa, except that we did not find Kelp Gulls nesting in pastures (perhaps because sufficient preferred habitats are available in Africa).

CONCLUSION

We have described a method for comparing nest sites with potential sites within a territory. We propose that individuals who nest in colonies do not have free choice of all nest sites potentially available, but are constrained by those features within their territory. By comparing their choice of particular features among habitats and colonies it is possible to generalize about the major factors that appear to influence choice of nest site.

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