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HABITAT SELECTION IN MEW GULLS: SMALL COLONIES AND SITE PLASTICITY

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Abstract.—We studied colony-site selection of Mew Gulls (*Larus canus*) in a small geographical area of south-central Alaska to: (1) determine if the plasticity in habitat selection in one region reflects the wide range of habitats used throughout their world-wide range, (2) ascertain the relative importance of physiognomic aspects of vegetation to nest-site selection in different colonies, and (3) quantify the communality of these characteristics among sites. We found colonies on grass, rock, sand, and earth, on rocky and sandy islands in lakes and rivers, on several types of marshes (floating vegetation, creek bog, muskeg and open grassy marsh), on a rock dike, on a roof, and in spruce trees. In all colonies, the gull's habitat preferences differed from random with respect to some characteristics, but not necessarily the same characteristics in every colony. By comparing habitat choices among colonies, we identified the factors that were required for nesting or were ignored. The overall choice of nest-sites indicates narrow selection for some characteristics within a diversity of major habitat types, and indicates plasticity in colony-site choices, but not nest-site choice. This analysis provides a general method for assessing the relative importance of social and physical factors in colony- and nest-site selection. *Received 22 Sept. 1987, accepted 22 Feb. 1988.*

Selection of suitable breeding habitat is critical for most animals because it directly affects fitness (Partridge 1978, Cody 1985). Despite high mobility as adults, nest-site selection locks birds into a single location for weeks. Variation in reproductive success among habitats may be due to differential predation rates, environmental stresses (high tides, thermal stress), or social factors such as territorial disputes (Burger 1985). Faced by stress, a pregnant mammal can move to a safe location, and newborn mammals may be carried to safe sites. In most cases, however, avian parents are restricted to chosen nest sites for the duration of incubation, and except for precocial species, this commitment persists for several weeks after hatching. Habitat selection is critical particularly for birds with young that remain in or near the nest until fledging.

Available habitats often vary gradually along gradients, and populations distributed over a wide geographical range may benefit from behavioral plasticity with respect to colony- and nest-site selection. Birds with a wide geographic range may either use similar habitats in all regions or may select different sites from region to region (Cody 1985). Birds may select similar physiognomic characteristics despite differences in available vege-

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tation species, vegetation cover, substrate types, or other physical characteristics. Diversity of habitat preferences found over a wide geographic range suggests that a species might use a diversity of habitats within one geographic region. Birds may be plastic in their choice of overall habitat (marsh, forest, field), but require very specific features for suitable nest sites. Presumably, behavioral plasticity in general habitat choices is particularly advantageous in regions with short breeding seasons, limited or changing habitat, or both. In this paper we attempt to distinguish these levels of colony- and nest-site plasticity. Particular features of the habitat may be ignored, of minor importance, or of primary importance to a bird selecting a nest site. If the characteristic is completely unimportant, there should be no consistent relationship for that characteristic between the available habitat and where the birds nest (Fig. 1A, after Burger and Gochfeld 1986). If, however, the characteristic is important to birds in selecting a habitat, they could nest in areas with high values (Fig. 1B) or in areas with less of the particular features (Fig. 1C) than is available in the general area. If the characteristic is critical and the birds require specific characteristics, they may select a very narrow range of values despite the wider range of available characteristics (Fig. 1D).

Although this analysis could be used within a colony or nesting area, by comparing the mean value for nest-site characteristics with the mean for random points among several colonies, we believe it is possible to infer which characteristics are actually being selected by the birds, and what their preferences are. For example, in one colony with sparse vegetation, birds may select habitats with more vegetation than the average available, suggesting that they prefer heavily vegetated areas. However, in another colony with dense vegetation, they may select sites with less vegetation than average. In both cases, they may have selected sites with comparable vegetation cover. Our study examines habitat selection by comparing nest-site characteristics with random points (=available habitat) for several colonies.

The Mew Gull (*Larus canus*) provided an excellent opportunity to examine plasticity because it nests in a variety of habitats and has an extensive Holarctic distribution. In North America, Mew Gulls (*L. c. brachyrhynchus*) breed from western Alaska east to Hudson Bay, Canada (A.O.U. 1983), while the conspecific Common Gull (*L. c. canus*) nests across Europe and Asia from near the Arctic Circle south to the British Isles, Netherlands, the Black and Caspian seas, northern Mongolia, Kamchatka, and Kuriles (Godfrey 1979). In Alaska, Mew Gulls breed on many streams or lakes of the interior (Gabrielson and Lincoln 1959), and Sowls et al. (1978) estimated there were 5000 pairs of Mew Gulls in coastal Alaska, but their surveys did not cover the Anchorage area.

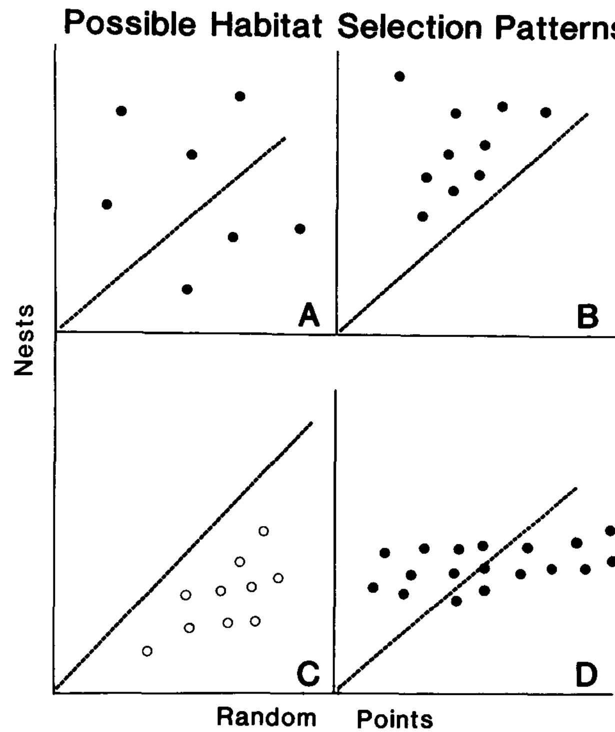

FIG. 1. Possible relationship of nest-site choices to available habitats (random points). Any variable (e.g., vegetation height) can be measured at nests and then at random points. Mean values for each are obtained at several colonies and plotted on a graph. Each point represents the mean value for nests plotted against the mean for random points for that colony (after Burger and Gochfeld 1986, see text for further explanation).

In this study, we examined plasticity in colony site selection in Mew Gulls in Alaska to: (1) determine if their choice of colony and nest sites in this area was as diverse as suggested from the literature, or whether a single population showed low plasticity, (2) determine the relative importance of physiognomic features of vegetation to colony- and nest-site selection, (3) determine the preferred or tolerated attributes that might influence habitat selection among colonies, and (4) determine whether certain characteristics are important in many different habitats. In a previous paper we examined nest-site selection in more detail and for additional characteristics (Burger and Gochfeld 1987). The main objective of this paper is to compare colonies to determine how gulls use each factor in colony-site selection.

In different parts of its range, *Larus canus* nests on a variety of substrates in a variety of habitats including grasslands, peat bogs, stone, rubble, sand, cliffs, and the tops of tree stumps (Dement'ev et al. 1951, Barth 1955, Hillis 1967, Isleib and Kessel 1973, Kumari 1976). *Larus canus* nests mainly in small colonies of up to 15 or 20 pairs (Bent 1921). In the interior of Alaska, Hurley (1931) found the species numerous on the Kuichak River with colonies up to 100 pairs, and Gabrielson and Lincoln (1959) and Sowls et al. (1978) mention only two coastal colonies as large as 250–300 pairs.

METHODS AND STUDY AREA

We studied 14 colonies of Mew Gulls within 250 km of Anchorage in south-central Alaska. Each colony was visited one to three times. We also observed two pairs nesting with terns in a lake and solitary pairs nesting in the tops of spruce trees. We made our observations from 26 June to 24 July 1985 during late incubation and early chick stages. At each colony site, we recorded a general habitat description, noted the dimensions of the colony and of the island or habitat type, and counted the number of adults and nests. For colonies with less than 30 nests, we collected data at all nest sites; for larger colonies (Hood Lake, Nenana River colonies A and B) we recorded data from 30 randomly selected nests. We used a table of random numbers to determine the coordinates of nests to be examined. Data collected at each nest included nest contents, distance to nearest tree or vegetation, height above water (or land), height of tree or vegetation, percent cover directly over the nest, percent cover in a one and five m circle around the nest, visibility of the nest from directly above, and visibility of the nest from five m. For the purposes of this study, vegetation height referred to plants that were not woody shrubs or trees, and tree height referred to woody shrubs and trees. Because the habitat varied among colonies, not all characteristics were represented at each colony.

At most colonies we identified a number of random points equal to the number of nests. The occupied area was treated as a rectangle, and the X and Y coordinates were selected from a random number table. At random points we measured the same characteristics as at the nests in that colony (Burger and Gochfeld 1986). We also used computer-generated random points to predict spatial features such as internest distance and distance to the edge of the colony. This Monte Carlo simulation procedure allowed us to streamline our collection of field data to the characteristics that were required at each site, thereby reducing the disturbance to the nesting gulls. The use of computerized Monte Carlo simulations to analyze complex events is now widespread (Ricklefs and Lau 1980). The simulations employ stochastic processes to generate "random" simulates analogous to the phenomenon being studied. From the simulation of 1000 replicates, we produced cumulative frequency distributions for nearest neighbor distance. The actual mean nearest neighbor distance for the colony was compared to the frequency distribution from which we could determine the likelihood of encountering a particular mean value if nests were indeed randomly distributed.

Within each colony, we compared the characteristics of the gull nests and random points to determine if gulls selected sites with particular features, compared to what was available. Among colonies, we compared the mean values for nests and random points (Fig. 1). Other nest-site characteristics and standard errors of the means can be found in Burger and Gochfeld (1987).

In this paper, we present mean values for nests plotted against the mean for random points for each nest-site characteristic in each colony. These comparisons reveal which characteristics are being ignored, maximized (or minimized), or highly selected within a narrow range (see Fig. 1). For each characteristic we used a Sign Test to test the null hypothesis that nest sites do not consistently have a higher or lower value than the random points. That is, an equal number of colonies should fall above and below the line of equivalent values. Not all features were present at all colonies, so we plotted on each graph only colonies where the characteristic was relevant. The detailed descriptive data used to calculate these means are presented elsewhere (Burger and Gochfeld 1987).

RESULTS

Colony-site selection.—We found 14 colonies of Mew Gulls in our study area, as well as two pairs nesting on a lake and two isolated pairs nesting in spruce trees (*Picea sp.,* Table 1). The number of nests per colony ranged from 2 to about 400 ($\bar{x} \pm SD = 59.6 \pm 105$, median = 22). Mew Gulls nested on islands in lakes and rivers, on marshes and bogs, rock dikes, on a roof top, and in trees. Nesting substrates included dry ground, grass, branches, and floating vegetation (Table 1).

Most sites were at least partially isolated by some barrier from ground predators and human disturbance (Table 1). The dry ground colonies were isolated by a lake, creek, highway, or fence. Within Anchorage, gulls nested on several dirt dikes that were enclosed by 3-m high chain link fence which excluded large mammalian predators and people. The riverine colonies were well-protected by the swift moving Nenana River or less so by the slow moving water of Snow Creek. The bog and marsh colonies were protected by water or sphagnum of varying depths, all difficult to negotiate. The rock dike colony was protected by a fence, and the roof colony was also within a fence and access required climbing a 9-m ladder. However, such protection did not exclude avian predators.

Snow Creek had the least protection from predators. Its colony on a sandbar was surrounded by moving water, but a highway bisected the island allowing mammalian predators access to the island. Numerous coyote tracks on the island and preyed-upon eggs indicated predation. For all other riverine and lake colonies a boat or white water raft was required to get to them.

Nest-site selection.—Eight of 10 colonies had larger mean inter-nest distances than inter-random point distances (Sign Test, $P < 0.05$, Fig. 2A). Nearest neighbor distance ranged from 120 to 800 cm, with a mean of less than 300 cm. Only in the Rock Dike and Hood Lake colonies did the nesting gulls aggregate. In both cases, gulls were pressed into the central area of the colony by tidal waters and human pressures (Rock Dike) or by air traffic in the water (float planes at Hood Lake). In both colonies, a few pairs nested near the edges or center of the colony, so we included these areas in our selection of random points. However, if we excluded

TABLE 1

NESTING HABITAT OF MEW GULLS IN SOUTH-CENTRAL ALASKA, 1985

Type	Habitat	Location (abbreviation for figures)	Number of nesting pairs	Isolation	Predation
Dry ground	Grassy island	Hood Lake, Anchorage (HL)	400	Surrounded by lake	People–monofilament line
	Small grassy islands with birch trees	Anchorage, Sullivan Park (SP)	24	Surrounded by lake	None
	Earth dike	Anchorage Military Base (MB)	20	Fenced (3 m high chain link)	None
	Landfill	Anchorage, Airport (AL)	25	Creek and highway (people near)	Cannibalism on eggs
Riverine	Gravel island	Mt. McKinley, Nenana River A, (NA)	30	Swift-moving river	None
	Rock island	Mt. McKinley, Nenana River B, (NB)	75	Swift-moving river	None
	Sand bar	Seward, Snow Creek (SC) (Mile Post 18)	80	Slow river and creek	Numerous coyote tracks, predated eggs
Wet ground	Wet marsh	Anchorage: Shell Oil plant floating nest	3	Water over 1 m deep	None
	Creek bog	Anchorage: Airport (CB)	12	Creek, water, and airport road	None
	Moss muskeg	Anchorage: Post Office (MM)	2	Water 1 m deep	None
	Open marsh	Portage Marsh (Mile Post 40 to Seward)	30	Shallow water (only site with shallow inundation)	None
	Open marsh	Potter's Marsh (Mile Post 10 to Seward)	18	Deep water	None

TABLE 1
CONTINUED

Type	Habitat	Location (abbreviation for figures)	Number of nesting pairs	Isolation	Predation
	Open marsh in lake	Tern Lake (Mile Post 90 to Seward)	2	Deep water	None
Rock	Rock dike	Anchorage, Port (RD)	30	3 m high chain fence and guard	People
Roof top	Fine gravel	Anchorage, Port Authority (RF)	13	9 m high building	None
Trees	Spruce trees	Denali National Park	2	Tree	None

these marginal areas, internest distances would have been greater than the mean distance between random points distances in these colonies as well.

Flooding is a real danger in both marsh and dry land colonies adjacent to water. In all cases, except for the Rock Dike colony, Mew Gull nests averaged higher above water than the random points (Sign Test, $P < 0.05$, Fig. 2B). Nevertheless, the mean nest site in several colonies (Nenana A and B, Moss Muskeg, Rock Dike, Creek Bog) was less than 0.5 m above water level. All of these colonies were exposed to tidal flooding (Rock Dike, Portage Marsh) or storm flood (the other colonies). Mean slope at random points in the colony sites varied from 0° (Portage Marsh, Moss Muskeg) to 34° (Military Base), yet the gulls always selected sites with lower slopes than the random points (Sign Test, $P < 0.02$, Fig. 2C). However, they did not always have the option to nest in places with slopes less than 10° because some colonies did not have flat places available (Military Base). Even at the Military Base, however, they nested on the flattest places, building up one side of the nest to make it level.

Mew Gulls in Alaska did not nest in completely unvegetated habitats (except for the Roof colony), although vegetation cover was sparse (<10% cover) in some colonies (Nenana A and B, Snow Creek, Rock Dike, Military Base). Vegetation cover consisted of trees (willows, alder, birch) and herbs (*Lupinus*, grasses).

The mean distance to the nearest herbs was always equal or less for nests than for random points (Sign Test, $P < 0.05$, Fig. 2D). Moreover the mean distance of nests to herb vegetation was always less than 0.5 m despite the available mean values of 0 to 6 m. Thus, distance to herb vegetation is an example of a characteristic having a restricted range. There was no clear pattern in the relationship between the mean distance from nests to trees and from random points to trees among the colonies (Sign Test, $P > 0.10$, Fig. 3A).

Vegetation height likewise showed a distinct relationship (Sign Test, $P < 0.02$, Fig. 3B). For nine of 10 colonies, mean herb height was greater around nests than at the random points. Portage salt marsh was the exception. However, marsh vegetation is usually higher where there is tidal inundation (see Montevecchi 1978), suggesting that spots with shorter vegetation would be those less vulnerable to tidal flooding.

Percent cover around the nest (within 0.5 m of the nest) was greater at the nests than at random points for 9 of 11 colonies (Sign Test, $P < 0.05$, Fig. 3C). Moreover, the cover over nests was generally greater than in the area within 5 m of nests (Sign Test, $P < 0.05$, Fig. 4A). Nenana A, where there was more cover near than over the nests, was the only exception.

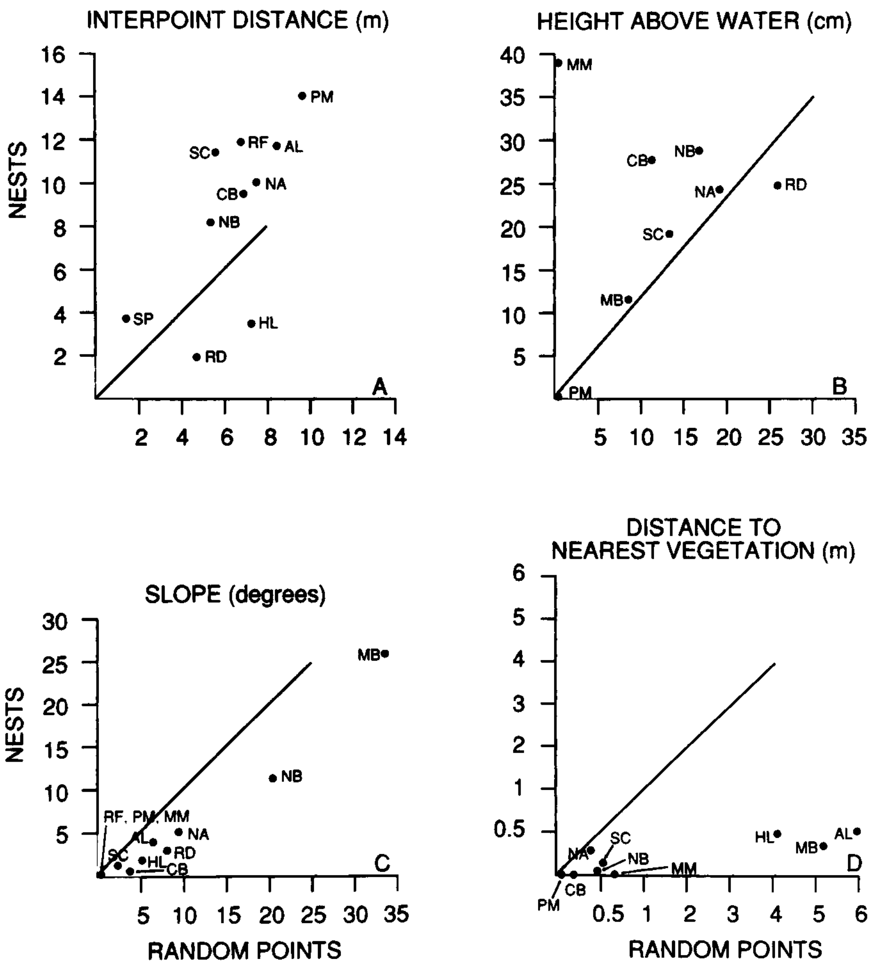

FIG. 2A. Relationship of mean nearest neighbor distance to interpoint distance of random points. AL = Airport Landfill, CB = Creek Bog, RD = Rock Dike, MB = Military Base, PM = Portage Marsh, NA = Nenana A, NB = Nenana B, MM = Moss Muskeg, RF = Roof, SC = Snow Creek, SP = Sullivan Park.

FIG. 2B. Relationship of mean distance above water of nests and random points for Mew Gull colonies.

FIG. 2C. Relationship of the mean slope in degrees at nest sites and random points for eleven Mew Gull colonies.

FIG. 2D. Relationship of mean distance to nearest vegetation (in meters) for nests and random points for nine Mew Gull colonies.

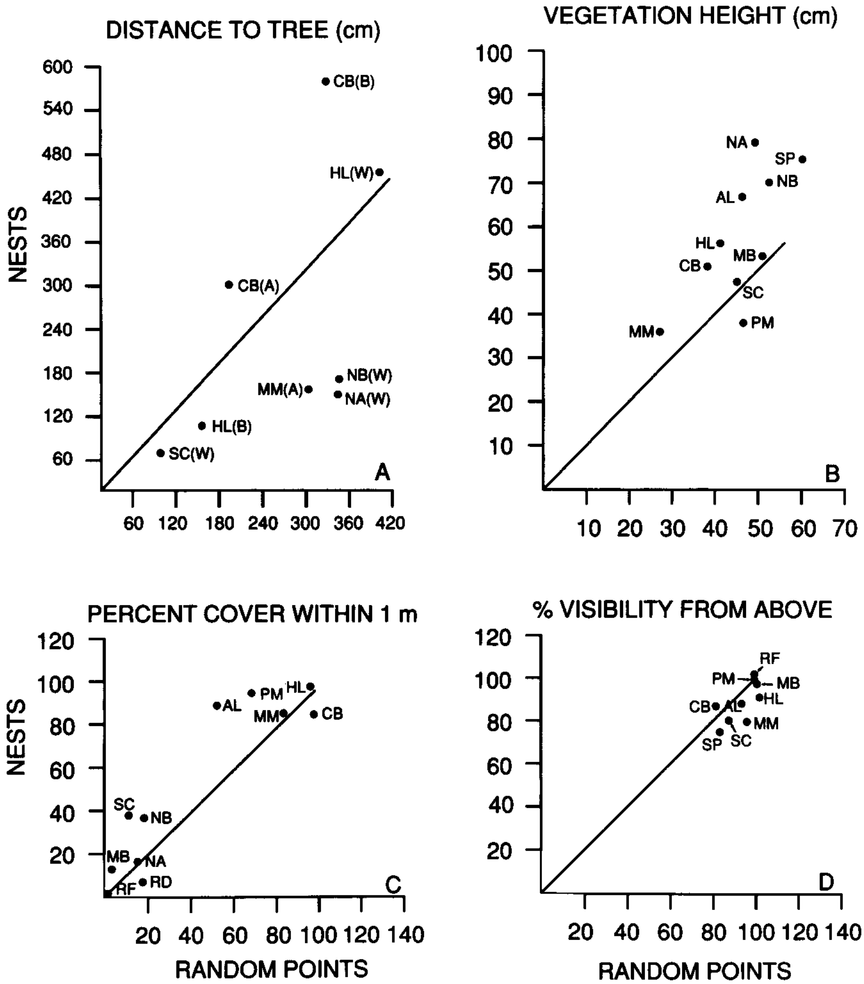

FIG. 3A. Relationship of mean distance to nearest tree (in cm) for nests and random points for nine Mew Gull colonies (W = Willow, A = Alder, B = Birch). Symbols the same as in Fig. 2.

FIG. 3B. Relationships of nests versus random points for ten Mew Gull colonies with respect to mean vegetation heights (in cm).

FIG. 3C. Relationships of nests versus random points for 12 Mew Gull colonies with respect to mean percent cover around nests.

FIG. 3D. Relationship of nests and random points in eight Mew Gull colonies with respect to mean visibility from above the nest (percent).

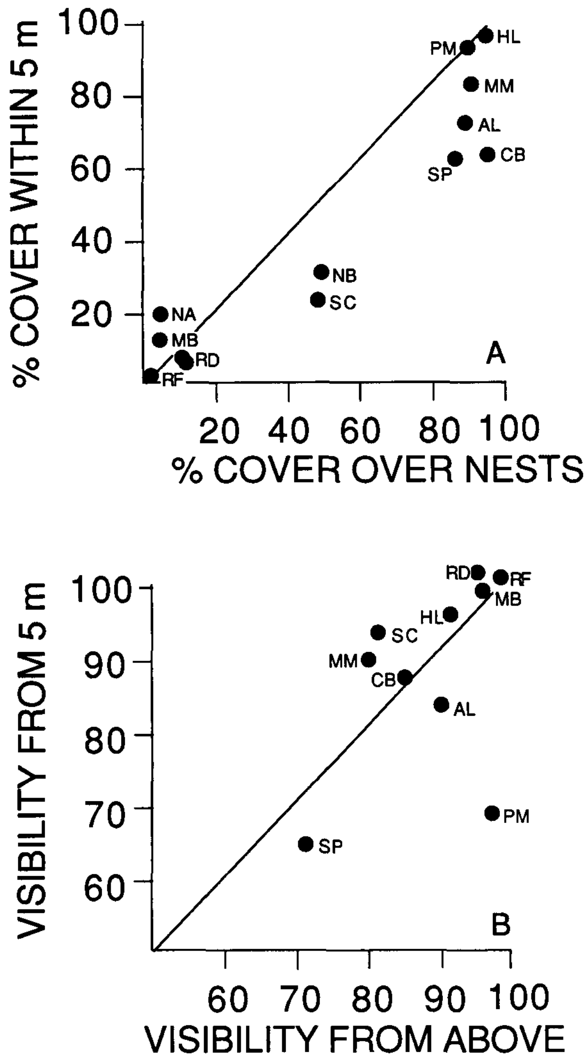

FIG. 4A. Relationship of mean percent cover over nests to mean percent cover within 5 m of nests for 12 Mew Gull colonies in Alaska. Symbols the same as Fig. 2.

FIG. 4B. Relationship of visibility from above to visibility from 5 m for nests in 10 Mew Gull colonies.

Vegetation cover and height are features that determine protection from inclement weather and predators. However, visibility is a more direct measure of vulnerability to aerial predators. A nest that is highly visible from above presumably has a greater risk of aerial predation. Generally visibility from above was less for nests than for the random points (Sign Test, $P < 0.05$, Fig. 3D). The Creek Bog was the only exception, because random points were usually within vegetation (low visibility), whereas all gull nests were on the top of tussocks (high visibility) secure from flooding but conspicuous.

We compared the visibility from above (exposure to aerial predators) with visibility from 5 m (exposure to ground predators such as coyotes, Sign Test, $P > 0.10$, Fig. 4B). In general, visibility was greater from 5 m (6 colonies) than from above (3 colonies), suggesting greater protection from aerial predators (see below). Mew Gulls selected areas with significantly more cover and taller grass and herbs.

DISCUSSION

Plasticity in colony selection.—Near Anchorage, Alaska, Mew Gulls nested in a wide variety of habitats including rooftops, marshes, bogs, sandy and rocky islands, dirt and rock dikes, and spruce trees.Vermeer and Devito (1986) also report Mew Gulls nesting solitarily on pilings in British Columbia. To our knowledge, this diversity of habitats is greater than that reported for any other gull in one geographical area and represents virtually the complete spectrum of gull nesting habitats except for deserts (see Howell et al. 1974) and true cliffs (Burger 1974).

The habitats where we found Mew Gulls nesting in south-central Alaska have been used elsewhere in its geographical range, but within smaller areas, *L. canus* generally uses only a few habitat types. The behavioral plasticity observed in Alaska may reflect a variety of selection factors including: (1) limited availability of preferred habitat, (2) small patches of preferred sites, (3) restricted breeding season forcing birds to select sites quickly, or (4) limited food resources restricting the location and size of colonies.

Colony size.—It is not apparent why Mew Gulls in Alaska and elsewhere form small colonies when most other gulls, even those nesting in highly disturbed sites, nest in larger colonies. Sowls et al. (1978) listed the population size of 41 coastal Alaskan colonies as ranging from 1 to 300 pairs (mean = 42 pairs, median = 20 pairs). About 10% of coastal colonies had more than 100 pairs. Turner's (1885) account of large Mew Gull colonies on cliffs in the Aleutians is surely erroneous as the habitat he describes is that of kittiwakes (*Rissa* spp.), and the recent coastal seabird surveys show virtually no Mew Gull nesting in the Aleutian chain (Sowls et al.

1978). In Europe, the conspecific Common Gull does nest in larger colonies (Cramp et al. 1974).

Current theory suggests that patterns of habitat occupancy should be linked to variations in individual fitness and that preferred habitat should be fully saturated unless the species is rare (Fretwell and Lucas 1969). Competitive interactions with other species, however, may modify habitat use (Wiens 1985). If preferred habitats were limited gulls might nest in suboptimal habitats or even forego breeding.

One interpretation for the small size of Mew Gull colonies is that suitable colony sites are small. In Alaska, most of the larger inland colonies (Hood Lake, Nenana River, Snow Creek) had insufficient space for other pairs, and the availability of high spots free from flooding also may have been limiting.

In the intermediate-sized colonies, gulls either used most available space (Sullivan Park, Rock Dike) or used most suitable sites with vegetation (Anchorage Military Base, Portage Marsh). In Sullivan Park, for example, every island that was high enough to escape flooding had a pair of nesting gulls, and the larger islands had two pairs. In the Portage Marsh, nest sites were vulnerable to flooding and some nests had been washed out. To increase use of high sites, the gulls would have to tolerate increased density. At the Army Base, most of the dirt dike had no vegetation, and gulls nested only near vegetation. Of the intermediate-sized colonies, only the Landfill area appeared to have additional available space. However, that colony was suboptimal because it was not protected from mammalian access and contained a colony of Arctic Terns (*Sterna paradisaea*) that harassed the nesting gulls.

Likewise, the small colonies either had as many pairs as the available space permitted (Shell Oil plant) or the gulls used the few suitable sites above water levels (Creek Bog) or next to objects that would provide suitable protection from wind (Roof).

Another indication that limitation of suitable sites has selected for behavioral plasticity in colony site selection was the diversity of nest sites used in adjacent areas. For example, the Roof colony was 75 m from the Rock Dike colony, and the Roof colony may have represented overflow from the Dike colony. Secondly, the Creek Bog colony was less than 100 m from the Landfill colony, and gulls may have nested on the suboptimal Landfill colony because no more suitable sites were available on flood-free grass hummocks.

Another possible factor selecting for behavioral plasticity is that a restricted breeding season in Alaska forces gulls to select colony sites quickly and nest, so that young are fledged before temperatures drop in August. In contrast, conspecifics elsewhere have a longer breeding season. The nesting areas we studied in Alaska were at 60–64°N latitude, while Common Gull nesting ranges in Britain, Germany, Poland, and Southern Sweden are mainly below 60°N latitude. Further, climatic conditions at the same latitude in Europe are milder than in Alaska because of the Gulf Stream. For example, tundra in Alaska occurs at 65°N latitude, while in Norway tundra is found at 70°N latitude. Over time, the colder climate and shorter breeding season in Alaska may select for sufficient behavioral plasticity to allow rapid, less narrow selection of colony sites compared to conspecifics in Europe. Further, gulls may nest in small colonies so the colony is less attractive or less visible to predators.

Lastly, limited availability of food resources could limit colony size in any location. However this seems an unlikely explanation for small colony sizes in Alaska, because gulls nested in different habitats within 100 m of each other where they were clearly using the same food resources. It is apparent that small scattered colonies are the norm for this species in Alaska (Gabrielson and Lincoln 1959, Sowls et al. 1978).

Overall, a few more pairs could have been inserted in most of these habitats, but in no case could the population have been markedly increased. Thus we suggest that a short breeding season, limited availability of colony sites, and the limited availability of nest sites free from the dangers of flooding, contribute to the pattern of the small colony size of New Gulls in Alaska.

Nest-site selection.—Plasticity of general colony-site selection may be possible only if the specific requirements of nest sites are met. In the following section, we examine whether there is behavioral plasticity in specific nest-site choices among colonies.

Gulls selecting nest sites could exhibit plasticity in their choice of social and physical features of the environment, or they could avoid nesting where site characteristics fall outside of a narrow range of preferred values. Some characteristics may be more important than others. Although comparing nest sites with available habitat in any one colony can be used to indicate statistical differences, only by comparing avian choices across colonies can one begin to distinguish which feature(s) of the environment the birds maximize or minimize, which they optimize, and which they ignore (refer to Fig. 1).

Once a bird chooses a colony site, it chooses a nest site within the colony. Thus the available range of characteristics is already fixed. By comparing several colonies where the range of values differs among colonies, we could examine the features selected under vastly different conditions.

Mew Gulls in Alaska selected nest sites that minimized some characteristics (slope, distance to vegetation, visibility from above), maximized some characteristics (distance above water, nearest neighbor distance, percent cover around nests), optimized some specific characteristics (distance to vegetation), and appeared to ignore others (distance to trees, vegetation height).

The different patterns of habitat use clearly indicate that Mew Gulls responded differently to the social and physical features of the environment. Given a particular range of available slopes, distance to vegetation, and visibilities from above, they always selected the lower range of values. Similarly, they chose to be farther above water and from neighbors and to have greater cover around the nest than was generally available. Regardless of the dispersion of vegetation reflected by the range of available distances to vegetation, Mew Gulls always nested at mean distances of less than 0.5 m from vegetation.

We believe our analysis can be useful for examining habitat selection of a wide variety of organisms in many different situations. Further the method can also be used to examine plasticity in a variety of laboratory experiments where animals are provided with a range of choices.

The present study clearly indicates that, although Mew Gulls show plasticity in their choice of habitat for colony sites, they minimize, maximize, or optimize particular features (within colonies). This results in their using nest sites that are protected from inclement weather and predators under a wide variety of habitat conditions.

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