NEST SITE SELECTION AND COMPETITIVE INTERACTIONS OF HERRING AND LAUGHING GULLS IN NEW JERSEY

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ABSTRACT.—We studied nest site selection and competitive interactions in a natural, unditched salt marsh colony of 5,000 pairs of Laughing Gulls (*Larus atricilla*) and 800 pairs of Herring Gulls (*L. argentatus*) in Barnegat Bay, New Jersey. Although Laughing Gulls have nested on this island for many years, Herring Gulls first nested there in 1964. Most Herring Gulls nested under *Iva* bushes, although some nested in *Spartina patens*. Early nesting pairs placed their nests in bushes while late-nesting pairs built randomly with respect to bushes and grass. Laughing Gulls nested primarily in *Spartina alterniflora* growth among many pools and pans, selecting the highest locations for nests. Early-nesting pairs nested on higher spots than late-nesting pairs. Nest site selection is a compromise between the conflicting selection pressures of tides, weather, cannibalism, predation, territorial behavior, and nest-building behavior. Nest requirements of these two gulls overlap up to 20% with respect to species of vegetation, elevation of sites selected, and vegetational characteristics. As Herring Gulls arrive and begin nesting before Laughing Gulls, and are considerably larger, they have a competitive advantage. The rapid increase of Herring Gulls on Clam Island suggests further competition as they spread into Laughing Gull nesting areas, leading to possible displacement of Laughing Gulls from this and similar islands.—*Received 18 February 1977, accepted 9 May 1977*. This paper was subsidized by the New Jersey State Mosquito Commission.

MOST species of *Larus* gulls nest colonially. Descriptions of their nesting habitat usually mention only the terrain (e.g. cliffs, dunes, beaches) and the species of vegetation (e.g. Paynter 1949, Harper 1971, Davis and Dunn 1976). Detailed studies of habitat and its effect on nest site selection exist for monospecific colonies of Black-headed Gull (*L. ridibundus*, Patterson 1965, Burger 1976), Laughing Gull (*L. atricilla*, Bongiorno 1970, Montevecchi 1975), Brown-hooded Gull (*L. maculipennis*) and Franklin's Gull (*L. pipixcan*, Burger 1974a, 1974b). Yet larids frequently nest in mixed species colonies in unpredictable combinations. For example, Lesser Black-backed Gulls (*L. fuscus*) nest with Herring Gulls (*L. argentatus*, Brown 1967, MacRoberts and MacRoberts 1972); Ring-billed Gulls (*L. delawarensis*) nest with California Gulls (*L. californicus*, Vermeer 1970) and Herring Gulls (Southern 1970). Although some authors allude to differential use of habitat in such colonies (e.g. Vermeer 1970), habitat partitioning among the nesting gull species has not been examined in detail. Similarly it is often difficult to determine from the literature whether the colonies consist of the nests of several species randomly dispersed or clustered, or are monospecific colonies placed side by side.

Herring Gulls have increased their numbers and expanded their breeding range since the turn of the century. The New England population has increased by a factor of 15 to 20 (Kadlec and Drury 1968, Drury and Kadlec 1974) and has extended its breeding range south to North Carolina (Hailman 1963, Parnell and Soots 1975). Their expansion in breeding range has been followed by expansion into salt marsh habitat (Parnell and Soots 1975, Burger 1977a). Consequently Herring Gulls now nest in habitats used by other larids such as Common Terns (*Sterna hirundo*) and Laughing Gulls. As early as 1943, Noble and Wurm reported Herring Gulls nesting with Laughing Gulls in a sand dune colony at Muskeget Island, Massachusetts, where Laughing Gulls used more densely vegetated areas, and Herring Gulls used more open sandy spaces. Laughing Gulls eventually disappeared from this island (Nisbet, pers. comm.). An increase in Herring Gulls in New England colonies has been associated with a decrease in breeding populations of Laughing Gulls and Common Terns (Drury 1965, Nisbet 1971a, 1973). Further, when Herring Gulls moved into North Carolina they tended to nest in colonies with Laughing Gulls and terns (Parnell and Soots 1975), and although Laughing Gulls nested in low *Spartina patens* swales, if Herring Gulls were absent, Laughing Gulls nested in higher places. This suggests that Herring Gulls prevented the Laughing Gulls from nesting on the higher, drier spots. Despite suggestions of the detrimental effect of Herring Gulls on other larids, little evidence exists to document habitat overlap, competition, or their resultant effects.

Although Laughing Gulls have nested on Clam Island, Barnegat Bay, New Jersey for many years, the first Herring Gulls nested there in 1964 (Rogers 1965). In 1976, we examined the nesting behavior of 5,000 pairs of Laughing Gulls and 800 pairs of Herring Gulls on Clam Island. We were especially interested in documenting the factors affecting nest site selection in each species, competition between the species, and habitat partitioning. We hoped to be able to predict the effects on Laughing Gulls of further increases in Herring Gull populations.

Methods and Study Area

Clam Island is a 130-acre salt marsh island in Barnegat Bay, New Jersey (39°45′N, 74°08′E). Although 12 of 259 salt marsh islands in the bay contain Herring Gull colonies, Clam Island is the only one containing both species. Several channels cut the island into four major subislands. Slight differences in elevation result in differences in tidal inundation and the attendant vegetation (Fig. 1). Predominant vegetation is *S. alterniflora* (51%) and *S. patens* (20%). Higher land along the island edges has bushes of *Iva frutescens* and *Baccharis halimifolia* (4%) with a maximum height of 1.5 m. Ponds normally cover 25% of Clam Island.

We made observations from 15 April to 1 June 1976. Ground and aerial surveys by helicopter allowed us to select sample plots representative of variations in the habitat. We checked all plots 3 to 5 times a week during the study period. For analysis of vegetational characteristics effecting nest site selection, we compared data from nests initiated during the first 2 weeks of egg laying for each species: Herring Gull (13–27 April), Laughing Gull (9–23 May). At this time we recorded: species of nest owner, clutch size, egg size, nest size, species of plant surrounding the nest, percent of bush cover, height of bushes, percent of total grass cover, percent of live and dead grass cover, mean height of grass cover, mean height of live and dead grass cover, distance to nearest neighbor, and distance to water. We collected similar data from an equal number of random points in the sample plots themselves. We therefore compared nest site selection within sections of Clam Island involving the colonies of each species rather than from the whole island to avoid confusing colony-site selection with nest-site selection. For analysis of early- and late-nesting birds we gathered data throughout the nesting period. For analysis of the marsh elevation of nest sites, we gathered data at the end of the nesting period to insure that we obtained the full range of elevations used by the gulls.

Absolute elevation in salt marshes is difficult to determine as tidal action constantly changes the water level. Therefore we determined a relative elevation by designating a fixed point in the marsh as zero, and measured elevations with a Leitz self-levelling level in 0.10 ft, which we later converted to cm. Relative marsh elevations ranged from 6 to 52 cm. We then determined the elevation of all nest sites in a 20-m wide transect from the lowest to the highest parts of one of the islands containing bushes, while recording the species of gull nest and the vegetation species surrounding the nest. We also sampled two other plots with nesting Laughing Gulls representative of the available *alterniflora* habitats, measuring grass height, nest size, and relative elevation of the nest rim of Laughing Gull nests. We gathered similar data from an equal number of random points in these two sample plots. We did not take similar elevation data from Herring Gull nesting areas as vegetation there was heterogeneous.

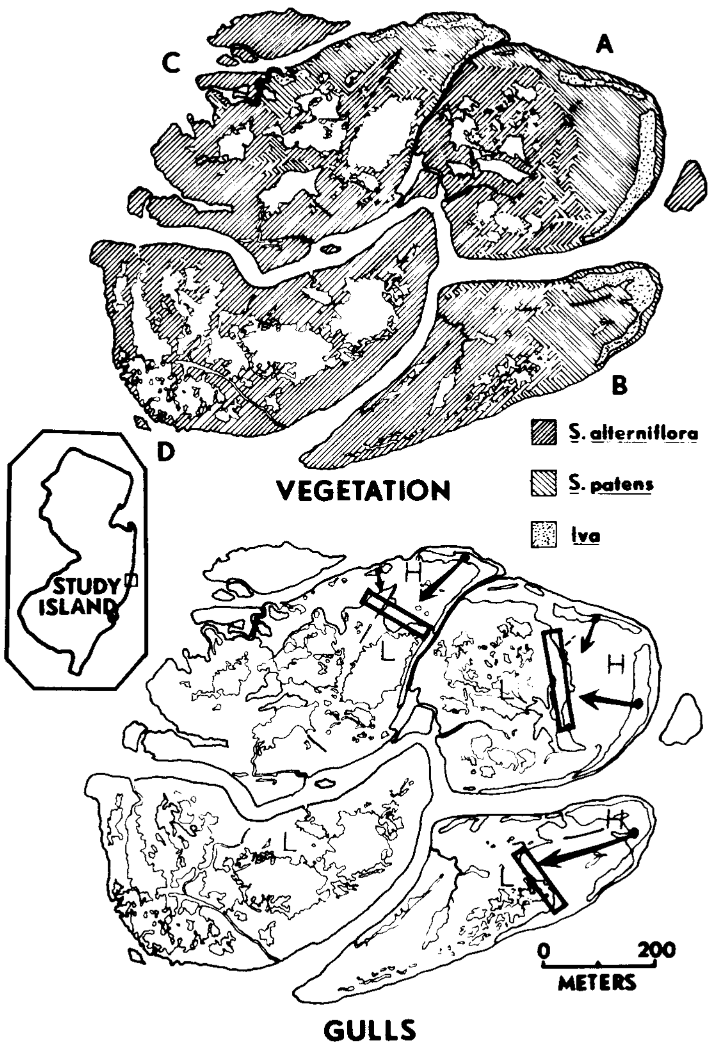

Fig. 1. Map of Clam Island, New Jersey showing the vegetation distribution with the rectangles representing areas of overlap in Gull populations. H = Herring Gull, L = Laughing Gull.

We used student's t-tests, chi-square tests, and correlation analyses where applicable, accepting probability levels of only below 0.05 as significant. Unless otherwise noted, standard deviations follow the means.

RESULTS

NEST SITE SELECTION IN HERRING GULLS

Breeding chronology and colony site selection.—Herring Gulls, present in the region all winter, begin to arrive on the nesting ground in early to late March. Initially gulls formed courting "clubs" (Tinbergen 1956), later moving into nearby ground to establish territories. Scattered nest scrapes appeared in early April, and nests were well formed by 11 April, although egg-laying did not begin until 14 April.

TABLE 1

PERCENT COMPOSITION OF SUBISLANDS OF CLAM ISLAND IN 1975

	Subislands[1]			
	A	B	C	D
Spartina alterniflora	42	50	47	64
S. patens	32	27	23	1
Iva and *Baccharis* bushes	9	6	4	1
Phragmites	1	–	–	–
Water	16	17	26	34

[1] Letters refer to Fig. 1.

The peak of egg-laying occurred from 20 April to 10 May, although the last eggs were laid on 30 May.

Herring Gulls nested on all four subislands (Fig. 1, Table 1) although they concentrated on subislands A (284 nests), B (246 nests), and C (235 nests). These subislands contained less than 50% *alterniflora* whereas subisland D, with only 3 Herring Gull nests, was primarily *alterniflora* and water. Nesting centers began in the bushes, and expanded outward into the surrounding *patens* growth (note arrows on Fig. 1).

Nest site selection.—Herring Gulls nested at relative elevations of 31 to 52 cm. They always nested in *patens*, frequently under bushes. We analyzed and compared the physical characteristics of 80 Herring Gull nest sites with 80 random points within the study area (Table 2). Eighty-two percent of the gulls nested under bushes compared to 15% for the random points. Gulls nested where the mean bush cover was 27% although dense bushes with 100% cover occurred nearby. Thus the gulls chose to nest in places with some bush cover, but not in those with complete cover.

We examined the Herring Gulls' use of bushes as a function of egg-laying date. Of

TABLE 2

NEST SITE COMPARISONS

A. Mean nest site characteristics compared to those of random points are given as means ± 1 SD.

Laughing Gull (n = 80)	Gulls	Random	df	χ^2	P
% Bush cover	0	0	–	–	–
% Old grass cover	23.2 ± 12.7	43.2 ± 14.8	9	145.30	.001
% Green grass cover	67.0 ± 17.7	54.4 ± 15.2	9	521.00	.001
Maximum grass height (cm)	31.4 ± 6.2	36.2 ± 9.8	5	46.38	.001
$\bar{X}$ grass height (cm)	26.7 ± 4.1	23.5 ± 5.7	5	15.10	.01
$\bar{X}$ old grass height (cm)	20.3 ± 3.2	23.4 ± 7.6	4	11.41	.05
$\bar{X}$ green grass height (cm)	26.5 ± 2.1	23.0 ± 4.3	3	14.29	.01
Herring Gull (n = 30)					
% Bush cover	27.9 ± 13.6	1.5 ± .1	9	2,585.70	.001
% Old grass cover	56.3 ± 31.8	61.2 ± 35.2	9	54.15	.001
% Green grass cover	28.1 ± 21.1	35.0 ± 31.8	9	126.69	.001
Maximum grass height (cm)	50.8 ± 15.9	29.0 ± 11.6	9	136.30	.001
$\bar{X}$ grass height (cm)	29.2 ± 6.4	21.5 ± 5.8	5	116.38	.001
$\bar{X}$ old grass height (cm)	35.8 ± 17.8	16.4 ± 9.9	5	380.00	.001
$\bar{X}$ green grass height (cm)	20.7 ± 10.7	17.3 ± 9.2	5	9.07	NS

B. Comparison of Herring and Laughing Gull nest site characteristics.

	df	t	P
% Old grass cover	158	8.65	.001
% New grass cover	158	12.65	.001
Maximum grass height (cm)	158	10.34	.001
$\bar{X}$ grass height (cm)	158	2.93	.01
$\bar{X}$ old grass height (cm)	158	7.66	.001
$\bar{X}$ green grass height (cm)	158	4.76	.001

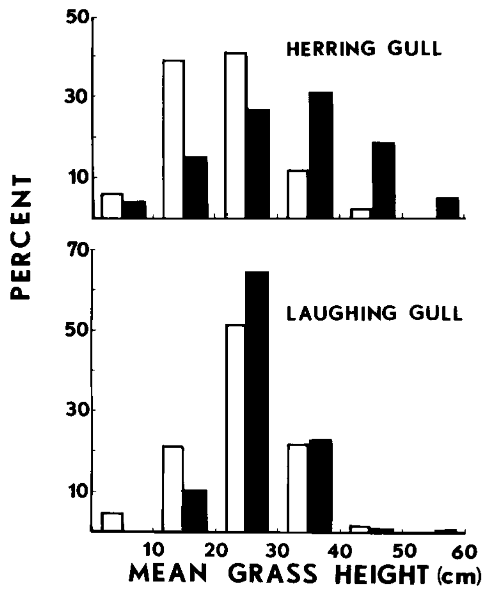

Fig. 2. Comparison of the mean percentage of cover and mean height of grass (solid bars) in 1-m plots around gull nests with random plots (open bar).

95 early-nesting pairs (13–22 April), 95% placed their nests in bushes ($\chi^2 = 825$, df = 1, $P < 0.001$), 68% of 156 mid-nesting pairs (23 April–10 May) built nests under bushes ($\chi^2 = 346$, df = 1, $P < 0.001$), and 10% of 34 late-nesting pairs (11–30 May) built nests under bushes ($\chi^2 = 3.39$, df = 1, NS). Thus only late-nesting birds nested randomly with respect to bushes. Behavioral studies from a blind showed that late-nesting gulls tried to set up territories in the bushes, but territory-holding gulls defended these tracts and forced late-nesting birds into open ground. Gulls nesting in

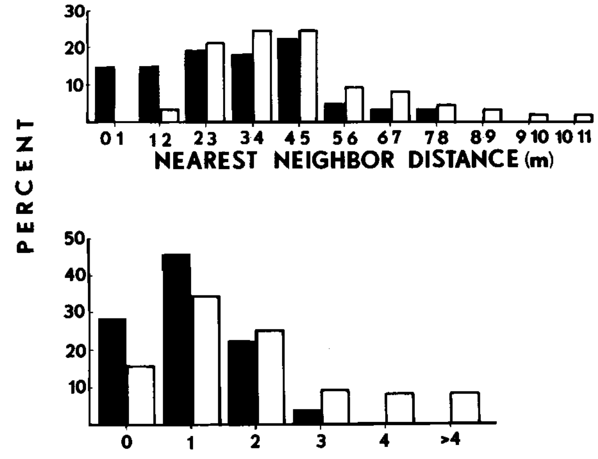

Fig. 3. Comparison of number of nests within 5 m and nearest neighbor distance for Herring Gulls (open bar) and Laughing Gulls (solid bar).

the sparse bushes (cover less than 40%) laid significantly larger eggs (t = 2.13, df = 142, $P < 0.05$) than those nesting in grass or dense bushes (over 41% bush cover). For this analysis we used only eggs laid from 20–30 April to eliminate size differences caused by seasonality or replacement clutches.

We then compared the mean percentage of cover and mean height of grass in 1-m plots around gull nests with those of random 1-m plots (Table 2). Herring Gulls chose nest sites having significantly lower percentages of dead and green grass, but significantly taller total grass height and mean dead grass height than that of the random plots (Fig. 2).

Although some Herring Gulls nested solitarily at least 100 m from other gulls, most nested close to conspecifics. Generally solitary birds nested on subisland D where each pair nested under isolated *Iva* bushes. In the main Herring Gull colony area, the distance to a nearest neighbor ($\bar{X}$ = 4.6 ± 2.3 m) was significantly less (t = 6.37, df = 158, $P < 0.001$, Fig. 3) than if the gulls were randomly distributed.

Nest Site Selection in Laughing Gulls

Breeding chronology and colony site selection.—Laughing Gulls migrate into New Jersey in early April, and begin flying sporadically over the nesting ground about mid-April. By late April they dotted the marsh, primarily defending territories in the early morning and late afternoon. Egg-laying began 9 May and continued until 2 June, although they initiated 75% of the nests from 12–21 May.

Laughing Gulls nested on all subislands, although the center of the colony occupied subisland D, which contained predominantly *S. alterniflora* with more open water than the others (Table 1, Fig. 1).

Nest site selection.—We analyzed and compared the physical characteristics of 80 Laughing Gull nests with 80 random points within the study area (Table 2). Most Laughing Gulls nested in *alterniflora* with significantly less dead grass cover and significantly more live green grass cover than that in the random plots. Similarly, nest plots contained significantly taller green grass and significantly shorter dead grass than in random plots. Although mean grass height in nest plots was significantly greater than in random plots, maximum grass height was significantly less at the gull nests (Fig. 2, Table 2). Laughing Gulls nested significantly closer (t = 3.21, df = 168, $P < 0.001$) to pools, pans, and creeks than the distance to nearest water from the random points ($\bar{X}$ = 4.5 ± 4.3 vs. 8.1 ± 5.7 m).

As Laughing Gulls nested in the lower *alterniflora* expanses of the marsh, we analyzed elevation differences in detail. The relative elevation of places where Laughing Gulls nested ranged from 7 to 36 cm. We were interested in seeing if they selected the highest spots for nest sites within any tract. In the lowest tract sampled, a tidal creek area where relative elevations ranged from 7 to 30 cm ($\bar{X}$ = 17.7 ± 3.6 cm, Fig. 4), Laughing Gulls selected sites significantly higher than random ($\bar{X}$ = 28.3 ± 2.4 cm, n = 170, χ^2 = 35.06, df = 5, $P < 0.001$). In both of the above tracts mean grass height in the plots selected by gulls was significantly higher than in the random plots (t = 2.63, df = 248, $P < 0.001$), but in the random plots relative marsh elevation did not correlate with grass height (r = 0.01, 0.11). Thus the gulls selected high elevations with tall grass. In both tracts sampled, nest depth negatively correlated with relative marsh elevation (r = 0.53, df = 78, $P < 0.001$; r = 0.33, df = 168, $P < 0.001$, Fig. 5). Although the range of elevations available varied between the two study tracts, the equations for the regressions are not signifi-

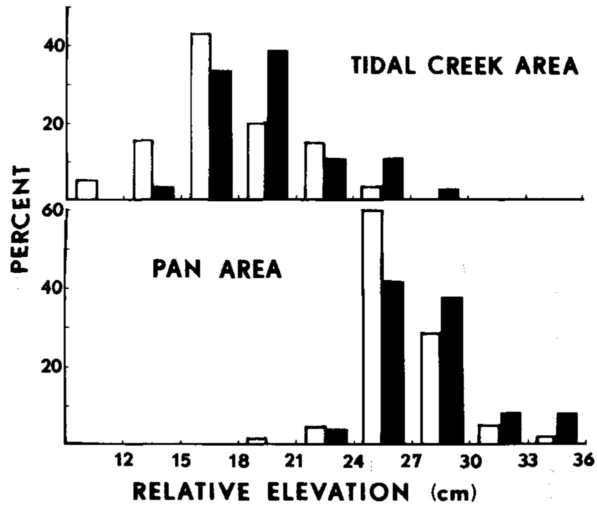

Fig. 4. Comparison of Laughing Gull nest site relative elevations (solid bar) with random relative elevations (open bar).

cantly different ($Y = -0.35X + .57$, $Y = -0.44X + .78$, $t = 1.6$, df = 130, Zar 1974). Thus gulls on lower ground built higher nests.

In another study area we examined the elevations selected by gulls as a function of egg-laying date (Fig. 6). Early (9–15 May) and mid-nesting gulls (16–21 May) selected significantly higher elevations than those of the random points ($t = 2.67$, df = 158, $P < 0.001$) and late nesters (22–30 May, $t = 3.66$, df = 106, $P < 0.001$). No differences occurred between the elevations selected by early- and mid-nesting gulls ($t = 1.32$, df = 88). We also compared the grass height of gull nests initiated early in the season with grass heights of these same nests during the first week after chicks hatched. Similarly we compared the grass height in the same random plots during the same time periods. The slight differences in grass heights of gull nests compared to

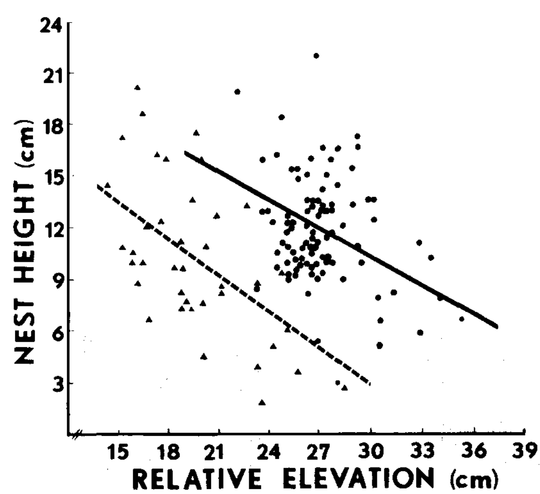

Fig. 5. Correlation of nest height with relative marsh elevation in the pan area (solid line) and tidal creek area (broken line) for Laughing Gulls.

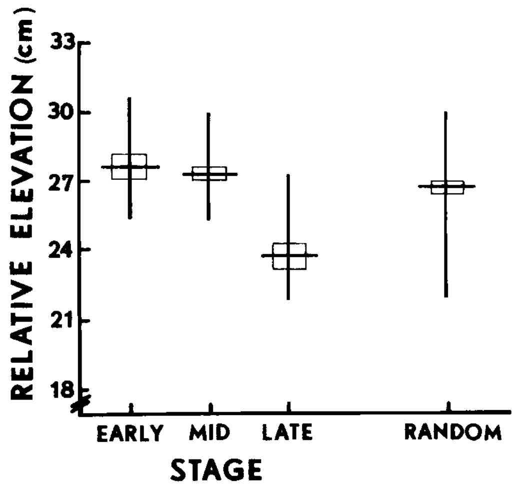

Fig. 6. Comparison of the relative elevations of the Laughing Gulls' nest sites as a function of egg-laying with random points (means = horizontal line, standard deviation = open rectangle, range = vertical line).

random points early in the season ($\chi^2 = 11.27$, df = 5, $P < 0.05$, Fig. 7) became accentuated later in the season ($\chi^2 = 55.7$, df = 6, $P < 0.001$). Thus selecting sites with slightly taller grass early in the season results in marked differences during the chick phase.

Laughing Gulls usually nested in clusters; solitary pairs were the exception. Mean nearest neighbor distances ranged from 0.6 to 7.2 m ($\bar{X} = 2.9 \pm 1.8$ m), and they nested closer to one another than predicted by chance ($t = 16.3$, df = 158,

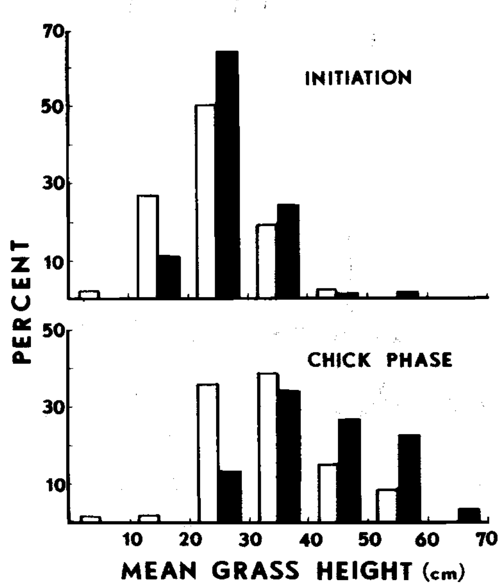

Fig. 7. Comparison of Laughing Gulls' nest site grass heights (solid bars) with random points (open bars).

$P < 0.001$). Although as many as six Laughing Gulls nested within 5 m of a nest, usually only one or two nested within this space (Fig. 4).

In sum, Laughing Gulls chose to nest in the highest parts of *S. alterniflora*, and built higher nests in lower places. They chose to nest in cover with significantly less old grass, more green grass, shorter old grass, and taller green grass than occurred in random plots.

DISCUSSION

Herring Gull nest site selection.—Herring Gulls nest in a variety of habitats including sandy or rocky islands, cliffs, sand dunes, grass meadows and *Spartina* salt marshes (Kadlec and Drury 1968, Harris 1970, Cramp, Bourne and Saunders 1974, Burger 1977a). Several authors allude to the vegetation in these colonies, but the factors determining nest site selection have not been described in undisturbed habitats. Burger and Shisler (1977) examined nest site selection in a ditched salt marsh, and found that Herring Gulls preferred to nest on the spoil piles that were higher than the surrounding *patens* marsh.

In the present study Herring Gulls chose to nest under sparse bushes with less, but taller grass cover than grew in the random plots. As is true of many behavior patterns (Tinbergen 1967), Herring Gulls' choice of nest sites represents a compromise between conflicting pressures relating to the acquisition and defense of territories on one hand, and protection from predators and climatic conditions on the other. Nesting under or near bushes is advantageous in a number of ways. Firstly, bushes grow in only the highest and driest parts of the marsh (Bourne and Cottam 1950, Kunz and Wagner 1957, Provost 1977). By nesting under bushes, Herring Gulls select the highest sites, which are also least susceptible to flooding. Nests in *patens* are also relatively safe from tidal inundation as this grass grows in places normally exposed only to flood tides. Barnegat Bay has only one main inlet at Barnegat Light, and the usual tide range on Clam Island is less than 0.5 m. Where the tide range is greater the *patens* marshes are inundated more frequently.

Secondly, bushes provide protection from adverse weather conditions such as rain, hail, and heat. Several authors have commented on these dangers to vulnerable gull and tern chicks (Austin 1933, Power 1964, Nisbet 1973, Burger 1974a, Gillett et al. 1975). Observations from a blind showed that on very hot days chicks of all ages moved under cover. Frequently all the chicks of one brood stood in the shade of one small *Iva* bush.

Thirdly, bushes provide cover from predators. Notorious as cannibals, Herring Gulls seem to prey on available, undefended, and easily observed chicks (Parsons 1971, Hunt and Hunt 1975, 1976, Haycock and Threlfall 1975). Chicks in cover are both less visible and wander less in search of cover from heat (unpubl. data). Similarly, other aerial predators such as Fish Crows (*Corvus ossifragus*) and Great Black-backed Gulls (*L. marinus*) flying over the island in search of eggs and chicks would be more likely to spot nests in the open than those under bushes. Gull chicks in cover remain closer to their nests and those not in cover seek out vegetation (Paynter 1949, Davis and Dunn 1976, this study). In several gulls and terns that normally nest amid vegetation, nesting success is higher in thick cover (e.g. Brown 1967, Lemmetyinen 1973).

To avoid the above-mentioned selection pressures (i.e. tides, weather, and predation) it seems advantageous to nest in dense bushes, which the Herring Gulls did not do. We believe that this relates to opposing factors related to territory acquisition and defense, and predator avoidance by the adults. When Herring Gulls first arrive at the colony site, they form courting "clubs" (Tinbergen 1953, 1956). As such groups require open spaces for displaying, these activities occurred in *patens* meadows. Once past courting, pairs and unmated adults moved into the nearest, less dense bushes to establish and defend territories. Early-nesters thus selected territories under bushes adjacent to open places. Gulls in bushes nest closer together because the vegetation provides visual barriers (Burger 1977b). Additionally, a Herring Gull with an edge territory can escape quickly if necessary. In dense bushes gulls cannot fly directly from their nests, but must walk to the edge before flying. Thus, nesting in dense bushes results in the adult being more vulnerable to predation. Moreover, while rushing madly through the bushes to avoid predators, wings and necks are easily tangled in the branches. We have caught adults in dense bushes, and have seen dead adults and young impaled on branches. Franklin's Gulls face similar problems in dense cattails, and similarly nest in the less dense edges (Burger 1974a). Herring Gulls nesting in *Iva* bushes on nearby islands also used the sparse edges rather than the dense interiors (Burger 1977a, Burger and Shisler 1977).

Gulls laid the largest eggs in the sparse bush growth. Older gulls normally lay larger eggs and clutches (Coulson 1966, 1968, Greenhalgh 1974, Ryder 1975), and egg size correlates positively with chick survival (Parsons 1970, Davis 1975). This suggests that older and more experienced birds with higher breeding success nest in the sparse bush growth.

Whereas the advantages of nesting near or under bushes relate to territorial behavior, predation, and climatic conditions, the advantages of nesting in sparse and tall grass relate to courtship and nest-building. To build a nest the pair must have a place to put it. In the early stages, pairs spend a great deal of time courting, and too much grass reduces visibility between members of the pair. Having less, but taller, grass provides a barrier or wall between adjacent nests while open spaces still remain for courting. Additionally, tall grass provides a ready hiding place for small chicks 1 to 4 days old. As most chick deaths occur during the first week (e.g. Haycock and Threlfall 1975), chicks need some cover if they are to survive.

Laughing Gull nest site selection.—Laughing Gulls nest in two types of habitats: dry islands with dense or scattered vegetation, and salt marsh islands (Bent 1921, Noble and Wurm 1943, Stone 1937, Buckley and Buckley 1972, Dinsmore and Schreiber 1974). Although these authors describe the nesting habitat, most state only in passing that the gulls nest in association with vegetation. Bongiorno (1970) examined nest site selection in this species by describing and manipulating vegetation at Stone Harbor, New Jersey. Similarly Montevecchi (1975) examined nest site selection in Laughing Gulls on Little Beach Island, New Jersey by comparing the habitat where they nested with random points. The colonies Bongiorno and Montevecchi examined were in *alterniflora* salt marshes where a high tidal range produced taller grass and more frequent flooding. Additionally, they both computed marsh heights by tidal water levels (see below). Nonetheless these studies provide excellent comparative material for nest site selection in salt marsh habitats. As Laughing Gulls are declining in the Northeast (Nisbet 1971a, 1971b) it is imperative to understand their nesting requirements to protect current populations adequately.

In the present study Laughing Gulls nested in *alterniflora* marshes with abundant open water in habitats similar to those Montevecchi (1975) and Bongiorno (1970) examined. *Spartina alterniflora* grows in the lowest marshes; it is the most seawardoccurring emergent plant growing at or close to mean sea level (Redfield 1972, Provost 1977). Thus, nests are exposed to frequent inundations, and slight advantages might be critical for survival. Possible differences in nest sites relate to elevation, vegetation, and placement.

Elevation is clearly a critical factor in nest site selection as, in general, lower sites flood more often than higher ones. In the present study Laughing Gulls nested on significantly higher places than occurred randomly. Montevecchi (1975) reported no difference in marsh elevation between gull nest sites and random locations. We believe this discrepancy is due to his method of determining marsh elevation. We determined elevations with accurate surveying equipment calibrated to a fixed point on the marsh, whereas Montevecchi determined elevations by recording the level of water during a high tide at particular nest sites and at random points. Tidal waters do not travel at the same speed nor deposit equal amounts of water over a marsh. On the contrary, vegetation impedes the flow of tide water so water depths depend partly on the amount of vegetation between the creek and the sample site. Secondly, the direction of the prevailing wind determines where on the marsh the tide is the deepest. Thirdly, elevation differences in the surrounding terrain affects tidal movement. That is, a low marsh surrounded by high elevations receives less water than one surrounded by low elevations. Fourthly, mere distance affects tidal movement as every 6 hours or so the tide reverses and places remote from tidal sources may not receive so much water. Nonetheless, determining tide levels by their method does reflect flooding conditions for the tides examined, and thus indicates which nests might be washed out.

Selecting the highest parts in the marsh for nesting obviously relates to tidal conditions. We also showed that early-nesting pairs selected higher sites than later nesting pairs. Later-arriving pairs find the higher places already occupied and thus are forced to nest in suboptimal spots. Thus nest sites may be limiting (see below), and in most years the later-nesting pairs would be less successful as eggs and chicks would be more exposed to high tides. Over many years nesting should be highly synchronous by the intense pressure to select a nest site early. This is the case: Laughing Gulls are more synchronous than most gull species (see Burger 1974a: 553).

Once a gull selects a site at a particular elevation, tidal factors can still be lessened by building higher nests. Nest height is correlated negatively with marsh elevation; Laughing Gulls built higher nests at lower elevations. Further, experimentation showed that artificially wetting and damaging nests resulted in immediate repair and nest building (Burger 1977c).

Laughing Gulls' selection of the highest parts in the marsh suggests that they use environmental cues in their selection. Vegetation is the most obvious feature, though we did not find a simple relationship between grass height and elevation. Montevecchi (1975) found an inverse relationship between grass height and ground elevation on Little Beach Island where the tidal range is greater. Considerably more work is necessary to relate grass height to elevation under varying tidal regimes before we can predict marsh elevation from grass height as accurately as the gulls can. The gulls receive additional information from tidal experience, as they arrive on the nesting ground to set up territories a month before they build nests (Bongiorno 1970, Burger and Beer 1975). During this time the gulls are exposed to very high tides, and presumably if the water reaches their body they move. Thus, behavioral information supplements environmental cues, but their determination of marsh elevations still results in selection of apparently unsuitable nest sites as washouts (tidal destruction

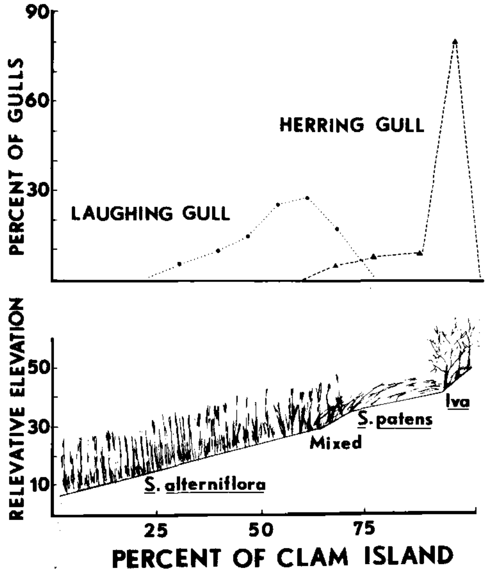

Fig. 8. Location of Gull populations in relation to relative elevation and vegetational distributions on Clam Island.

of nests and eggs) occur frequently in New Jersey marshes. Montevecchi (1975) reported washouts during 7 of the last 10 years at the Little Beach gull colony. The Clam Island colony does not suffer such a high washout rate as the tidal range is much less and a barrier beach island buffers it from violent winds.

Laughing Gulls on Clam Island selected nest sites with less and shorter dead grass cover and more and taller green grass cover. Such selection represents a compromise between tidal forces, territoriality, mobility, and predation. Taller grass is advantageous during high tides because it impedes water movement and prevents flooded nests from moving (Bongiorno 1970, Montevecchi 1975). In flood tides some Laughing Gull nests float, and tall grass anchors them in place. During exceptionally high tides we have seen nests with incubating gulls floating out toward the bay. Tall grass also provides excellent cover for protection against predators and climatic factors (see above), but it obstructs nest building and hampers the movements of courting adults and their ability to fly in and out easily. Thus it is advantageous to nest in some tall grass, but not in places completely covered with it. Nesting in new growth ensures that these sites will later have tall grass for the chicks to hide in.

Competition and habitat partitioning between Herring and Laughing Gulls.—In their spread southward, Herring Gulls have begun to nest in places heretofore used only by Laughing Gulls and terns, thereby causing decreases in these populations. Workers reporting on colonies during the early phases of Herring Gull invasion (e.g. Noble and Wurm 1943, Parnell and Soots 1975, Montevecchi 1975) note that the species use different habitats, but after many years the Laughing Gull and tern populations decline or disappear while the Herring Gulls continue to increase. Nisbet (1971a) squarely stated that the cause of Laughing Gull decline in the Northeast is the encroachment of Herring Gulls into their habitat.

In this paper we present data showing the mechanism of this displacement. A cursory look at Clam Island from a helicopter reveals that the two species overlap in only small parts of the marsh (Figs. 1, 8). Further, vegetational analysis of data for each species indicates that their respective requirements differ (Table 2). However, these data require further examination.

Figure 8 shows only a small area of overlap between the two species, but the peak of Laughing Gull nesting occurs very near the beginning of the elevations used by Herring Gulls. Taken by itself, this suggests that without the presence of Herring Gulls, Laughing Gulls might nest higher on the marsh, or at least that the curve would not be attenuated at this end. As higher nests have greater chances of success during storm tides, the foreshortening of this end of the curve eliminates nests most apt to be successful.

At present most Laughing Gulls nest in *alterniflora* and Herring Gulls nest in *patens*. Again, at first this suggests habitat partitioning, but on Clam Island six pairs of Laughing Gulls nested in *patens*, though only in restricted sites with no *Iva* bushes and thus no Herring Gulls. Secondly, scattered patches of *alterniflora* grow among the *patens*. Although these are the highest *alterniflora* growths in the marsh, they are used only by Herring Gulls. One such large expanse contained nesting Laughing Gulls in past years (F. Lesser, pers. comm.). Early in the season some Laughing Gulls flew over this marsh, landed for a few minutes, and were chased by Herring Gulls.

Habitat utilization in other gull colonies bears examination. Laughing Gulls nest in *patens* on nearby High Bar Island, Long Point Island, and Little Beach Island on Brigantine National Wildlife Refuge (pers. obs.), and in North Carolina (Parnell and Soots 1975). Similarly Herring Gulls nest in *alterniflora* at Little Beach and at five other neighboring islands (Burger 1977a), and on nearby Caravel Island (Burger, unpub. data). Thus, in terms of vegetation species, both gulls can nest in both *alterniflora* and *patens*.

We believe that on Clam Island, Laughing Gulls could nest, and might at one time have nested, on *patens* growing at higher elevations. Further, they certainly would nest in the scattered *alterniflora* patches if Herring Gulls were not present. Laughing Gulls are at a disadvantage in competitive interactions for two reasons: they arrive and nest later than Herring Gulls, and they are considerably smaller. Herring Gulls already have nests by the time Laughing Gulls arrive. As observing where conspecifics nest provides clues to possible nesting locations (Klopfer and Hailman 1965), Laughing Gulls would choose sites with Laughing Gulls and avoid those with Herring Gulls. Further, in aggressive interactions, larger species usually win over smaller species (see Morse 1974 for summary). Behavioral observations during April and early May support these contentions (Burger, unpub. data). Laughing Gulls often flew over territory occupied by Herring Gulls, landed, and left. In late April 23% of all aggressive interactions (n = 146) in the overlap areas involved both species. Herring Gulls chased all Laughing Gulls landing within 4 m of their stations, whereas Laughing Gulls chased only 18% of the Herring Gulls landing near their stations. Within 2 weeks, virtually no interactions occurred between the species.

Herring Gulls have doubled their population on Clam Island about every 2 years since they arrived in 1964. At this rate, they will soon require additional nesting space. This potential increase in their population size, coupled with the overlap in nesting requirements predicts they will move into Laughing Gull nesting territories. Their large size and early arrival gives them competitive advantages; their ability to breed successfully in places flooded by tides (Burger 1977a) means they will remain there. Taken together, these facts suggest that Herring Gulls will increase at the expense of Laughing Gulls and sooner or later force them out of Clam Island.

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