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Nest Site Selection and Its Survival Value Among Laughing Gulls

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Summary. 1. The nesting strategy as determined by nonrandom variation in environmental features at laughing gull (*Larus atricilla*) nests in a salt marsh was studied (Fig. 3). Gulls tended to nest on mats in tall grass that grows on low ground (just above high tides) near water (Figs. 4–7). Grass height was inversely related to ground elevation and distance to water (Fig. 8). Throughout the season, gulls selected nest sites in grass about 35 cm in height; due to continued grass growth, early breeders had taller grass around nests (Fig. 9). Pairs in the colony center nested earlier and in taller grass than pairs in a peripheral area.

2. Mats apparently stabilize nests during flooding, and by settling on mats gulls may conserve energy in the collection of nest material. Tall grass around nests afforded chicks protection from predators and weather, and held floating nests in place during flooding.

3. Gulls spend about 4 weeks (two spring tidal cycles) on the nesting grounds before egg laying. During this time they perform virtually no nest building and probably gain important information about nest site suitability.

4. Tidal flooding, the greatest threat to reproductive success – destroying 70–100% of the nests in the colony – occurred on average once every 2 years over 10 years. Floods occurred during spring tides accompanied by sustained NE winds.

5. Following a flood that destroyed 70% of the nests in the colony, it was shown that a significantly greater proportion of successful pairs nested on mats and in significantly taller grass than unsuccessful pairs. Grass height, especially that on the SW side of the nest, was the most important predictor of success during flooding.

6. More pairs in the central area were successful than those in the peripheral one: the result of nesting in taller grass and the greater protection of the central area from tides and winds. Though not differing among successful and unsuccessful nesters, females in the peripheral area laid smaller eggs and clutches, and laid later than females in the central area (over 3 years), suggesting that females in the peripheral area were on average

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younger than females in the central area. It was speculated that, on average, younger pairs will experience during flooding lower reproductive success as a result of nesting inexperience and nesting in suboptimal habitat. The smaller reproductive investments of younger pairs in eggs and clutches can be interpreted as an adaptation to conserve energy during a period of the life cycle when new behavioral adjustments and nesting areas are being explored.

Introduction

Animals tend to distribute themselves adaptively throughout their breeding habitats, though most demonstrations of this fact are for the most part correlative and have not been linked directly with reproductive success (Brown, 1975; Wilson, 1975; Barash, 1977). The selection of a nest site with regard to the environmental features of the breeding habitat is often a crucial determinant of avian reproductive success. Numerous studies of avian nesting location have proved informative in this regard (e.g., Ricklefs and Hainsworth, 1969; Heppleston, 1971; Williams, 1974), and some studies have shown further that differences among birds choosing different nesting sites correspond with differential breeding success (e.g., Gibo et al., 1976; Nettleship, 1972; Storey, 1978). In the present study the nest site preferences of laughing gulls (*Larus atricilla*) and the survival value, i.e., effects of behavior on reproductive success and fitness (Tinbergen, 1963, 1967, 1973), of these preferences were investigated.

Laughing gulls nest colonially on low-lying salt-marsh islands in many areas of their breeding range along the Gulf and Atlantic coasts of North America (Bent, 1921; Klopfer and Hailman, 1965; Bongiorno, 1970). The salt-marsh provides a relatively homogeneous habitat of meadows of *Spartina* grasses irregularly interspersed by winding tidal creeks, brackish pools, and mats of salt hay (Teal and Teal, 1969; Hiscock and Curtsinger, 1972; Redfield, 1972). As is the case for all ground nesting species in the salt marsh (Andrews et al., 1977; Storey, 1978), tidal flooding is the most serious threat to the gulls' reproductive success; embryonic mortality and losses to predators are small in comparison (Montevecchi, 1975, 1977, and unpublished data). Each year some nests are destroyed by tides, and in many years tidal floods destroy most nests, eggs, and chicks in the gullery.

The gull's nest site selection strategy as reflected in the nonrandom variation in habitat features at nest sites was the focus of the initial phase of the study. Then following a flood that destroyed most nests in the colony, a comparison of habitat features at successful and unsuccessful nests allowed for an empirical determination of the survival value of the gull's nest site selection behavior.

Methods

Research was done during 1971–1975 in one study area near the center of the densest nesting concentration and another near a peripheral extent of the nesting distribution of the gullery on the salt-marsh islands of the Brigantine National Wildlife Refuge, New Jersey, USA (39° 28′ N,

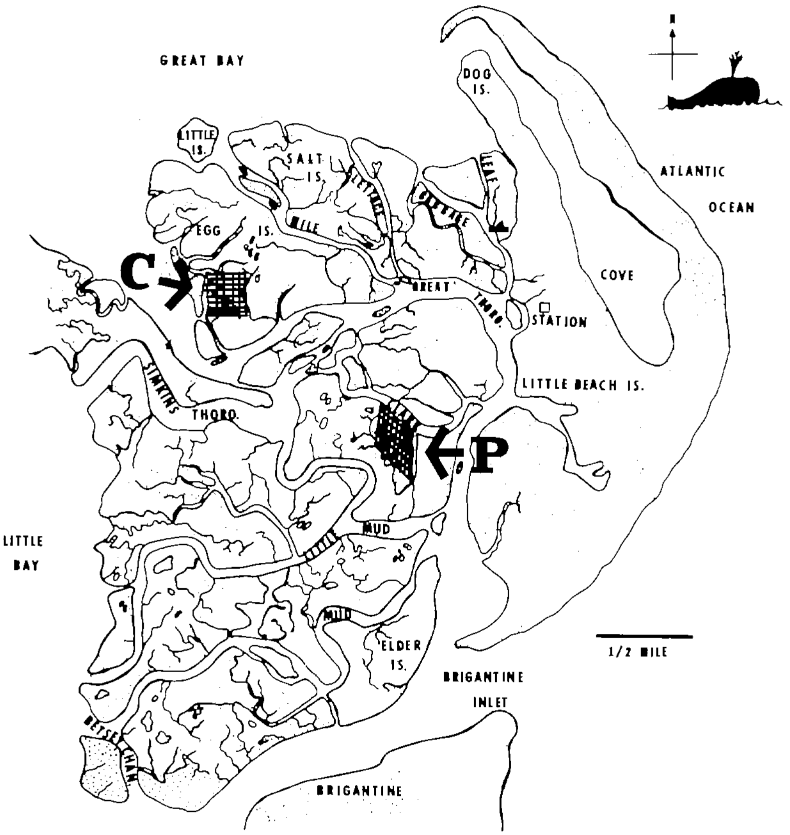

Fig. 1. Central (*C*) and peripheral (*P*) study areas in the gullery on salt-marsh islands of the Brigantine National Wildlife Refuge

74° 21′ W). Each study area was approx. 14 ha (Fig. 1). Other work was done in four 23 × 91 m quadrants in the gullery on Ring Island, Stone Harbor, New Jersey (39° 03′ N, 74° 47′ W; Fig. 2). Unless stated otherwise, procedures refer to work in Brigantine.

Line transects of fixed compass direction were set out in each area (Fig. 3), and provided for linear partitioning such that any site in the area could be designated by a pair of X-Y coordinates. For purposes of comparison with habitat measurements taken at nests, control data were collected at sites with randomly generated coordinates (see Burger, 1974). To minimize disturbance in the colony, control sites located in water and other inaccessible locations were not replaced; thus sample sizes of nest and control data are unequal.

During 1972–1974, areas were searched daily throughout egg laying, then every 2–3 days till hatching, when nests were again checked daily. Numbered markers were staked by nests, and the distance and type (creek or pool) of water body nearest each nest were recorded. The distance of the nearest *Spartina* mats (1 sq. m or more) from each site in Brigantine and on Ring Island was measured in 1974; distances greater than 30 m were scored as 30 m. The tallest grass in the N, E, W, and S quadrants around each site was measured and averaged. Grass measurements were obtained after hatching (July 1973), and as each nest was initiated (May–June) and during hatching (late June) in 1974. Site elevations relative to mean high water (MHW) were determined with portable tide gauges and computations developed by Andrews (1977).

Lunar phases (U.S. Nautical Almanac Office, 1964–65, 1968, 1970–1972), tidal heights (National Oceanic Survey records for Atlantic City, New Jersey) and wind speeds and directions (National

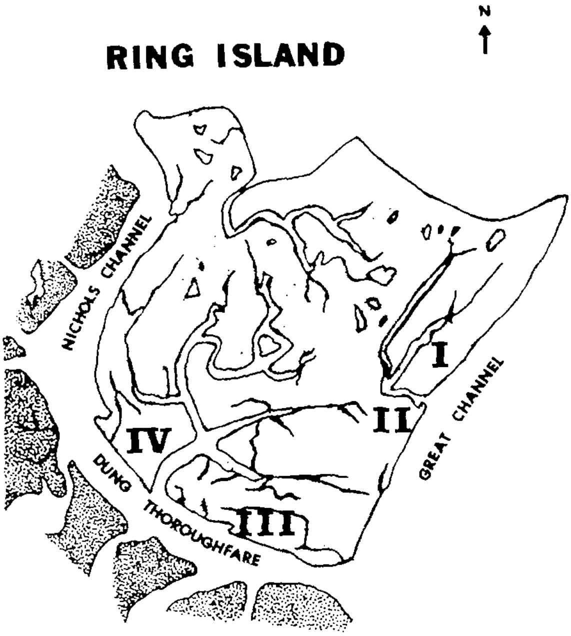

Fig. 2. Four study quadrants on Ring Island. Quadrants I, II, and III are located in areas where Bongiorno (1970) worked (see text)

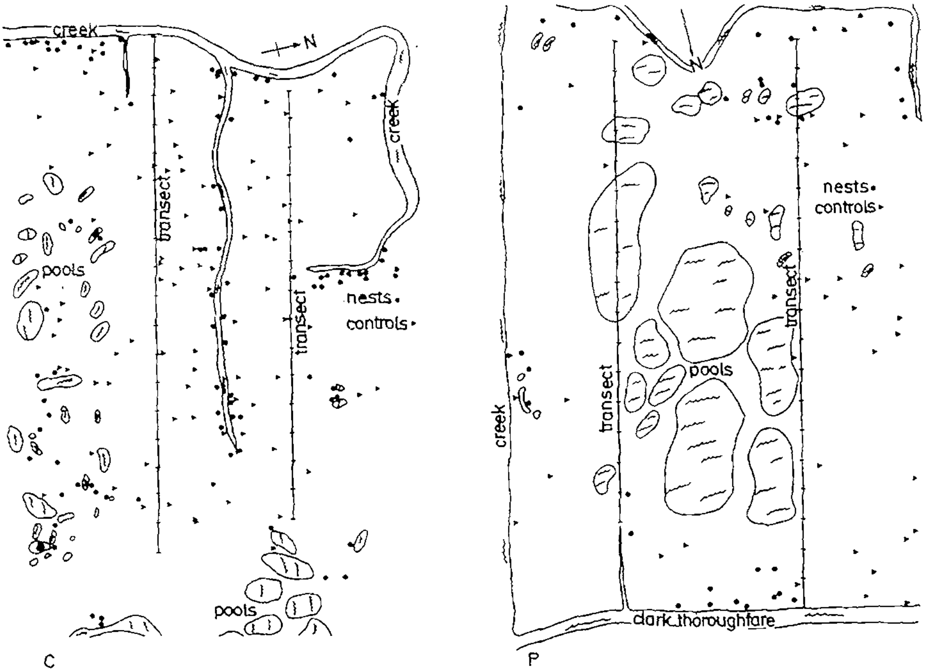

Fig. 3. Nests (circles) and controls (triangles) in the central (*C*) and peripheral (*P*) study areas in 1973; 15 m intervals on transects

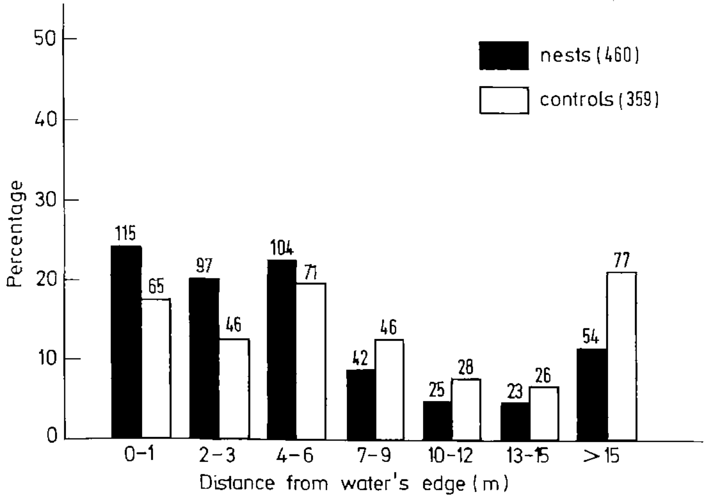

Fig. 4. Proximity of nest and control sites to mats. The *n* of each group is given at the top of the columns

Climatic Survey Records) during flooding that produced substantial reproductive loss during 1965-1974 and of Hurricane Agnes (1972) were tabulated and compared with appropriate monthly averages.

The fates of individual nests were determined following a flood on 24-25 June 1974. Nests were considered destroyed if (1) they were not located, (2) eggs were smashed or missing, or (3) the nest cup was flattened and no live chicks were found. Sites of unsuccessful nests were located by identification stakes and topographic features; exact sites were marked by patches of pale, stunted grass. Habitat measurements at successful and unsuccessful nests were compared. Censuses of nesting areas I and II on Ring Island (Fig. 2) were made before and after the flood. Egg laying dates (15 May = day 1, 16 May = day 2, etc.), clutch sizes, and egg measurements collected from 1972-1974 were also analyzed.

Results

1. Nest Site Selection

In general, the laughing gulls tended to nest on mats in tall grass that grew on low ground near water. The relationship of the gulls' nesting distribution to each of these factors is considered in turn. The gulls nested on (or near) *Spartina* mats (Fig. 4): 24% (33/137) of the nests were situated on mats compared with only 3% (3/100) of the control sites ($\chi^2 = 18.36$, $df = 1$, $P < 0.001$). There was no significant difference between the proportions of central (22/101) and peripheral (11/36) pairs that nested on mats. Compared with the colony in Brigantine, gulls showed a significantly greater tendency to nest on mats on Ring Island where 91% (446/493) of the nests were on mats ($\chi^2 = 255.58$, $df = 1$, $P < 0.001$); there seemed to be greater concentrations of mats on Ring Island. Proximity to mats showed a significantly positive correlation with inter-nest distance on Ring Island ($r = +0.40$, $df = 490$, $P < 0.001$), though not in the colony

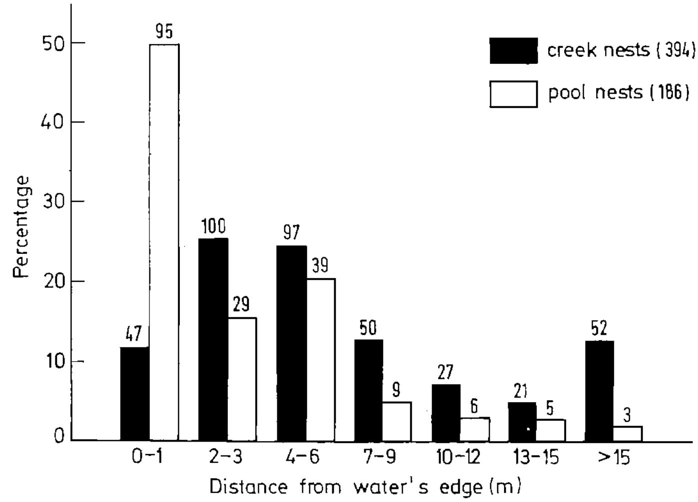

Fig. 5. Proximity of nest and control sites to water. The *n* of each groups is given at the top of the columns

Table 1. Nest placement in relation to water

Year	Mean (±SE) distance to water (m)				
	Nests	Controls	*t*	*df*	$P<$
1973	3.1±0.2	8.2±0.7	7.77	351	0.001
1974	5.1±0.4	10.3±1.0	5.43	234	0.001
Combined	4.0±0.2	9.0±0.6	8.98	586	0.001

in Brigantine. The proximity of nests to mats was significantly negatively correlated with distance to water ($r=-0.44$, $df=135$, $P<0.001$); 47% (20/43) of the pairs on high ground on Ring Island (area I) nested on mats compared with 94% (161/171) of pairs nesting on low ground (area II; $\chi^2=94.16$, $df=1$, $P<0.001$).

The gulls also nested near water (Fig. 5; Table 1), and pairs by pools nested significantly closer to water (2.7±0.3 m) than did pairs by creeks (4.8±0.2 m; $t=6.00$, $df=437$, $P<0.001$; Fig. 6). Gulls were about twice as likely to nest nearer to a creek than to a pool (290 vs. 149 nests), reflecting the proportions of these regions in the study areas. There appeared to be a higher ratio of creek to pool edge in the central area: 73% (127/174) of the controls in this area fell nearer to creeks than to pools compared with 33% (23/70) of the controls in the peripheral area ($\chi^2=57.34$, $df=1$, $P<0.001$), and over 3 years proportionally more pairs in the central (238/301) than in the peripheral area (52/138) nested nearer creeks ($\chi^2=70.48$, $df=1$, $P<0.001$). There was no correlation between nest proximity to water and dates of nest initiation ($r=0.02$,

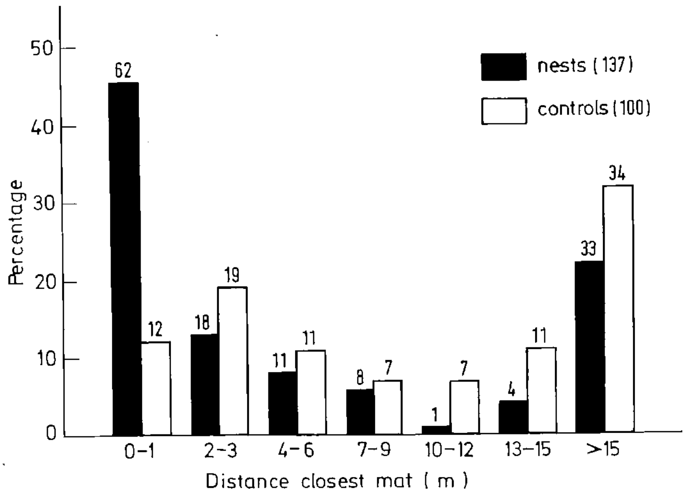

Fig. 6. Proximity of nests near creeks and nests near pools to water. The *n* of each group is given at the top of the columns

Table 2. Grass heights (cm) measured at nest initiation and after hatching (A) nests vs. controls, (B) nests near creeks vs. nests near pools, (C) controls in central area vs. controls in peripheral area, (D) nests in central area vs. nests in peripheral area

		Grass height	
		Nest initiation	Posthatch
(A)	Nests	33.8 ± 0.8	69.2 ± 1.2
	Controls	24.1 ± 1.3	46.8 ± 1.0
		$t = 7.14$, $df = 198$, $P < 0.001$	$t = 14.19$, $df = 428$, $P < 0.001$
(B)	Nests by creeks	36.6 ± 1.0	77.2 ± 0.8
	Nests by pools	29.0 ± 0.8	68.2 ± 1.4
		$t = 5.43$, $df = 106$, $P < 0.001$	$t = 4.54$, $df = 185$, $P < 0.001$
(C)	Central controls	29.8 ± 0.5	53.2 ± 0.6
	Peripheral controls	28.6 ± 0.9	53.9 ± 0.8
		$t = 1.00$, $df = 90$, $P < 0.05$	$t = 0.20$, $df = 150$, $P < 0.05$
(D)	Central nests	41.9 ± 0.4	92.5 ± 0.7
	Peripheral nests	35.8 ± 0.5	81.9 ± 0.7
		$t = 2.84$, $df = 106$, $P < 0.01$	$t = 4.54$, $df = 185$, $P < 0.001$

$df = 445$). The gullery was sparsely settled (Montevecchi et al., 1978, and much area adjacent to water was uninhabited.

Nests were built on low ground just above MHW (10.1 ± 0.03 cm). A comparison of nest and control data revealed that gulls in the peripheral area randomly selected ground elevations on which to nest.

Pairs also nested in tall grass (Table 2A; Fig. 7). Ground elevations and grass heights (at nest initiation *and* after hatching) at nests were significantly

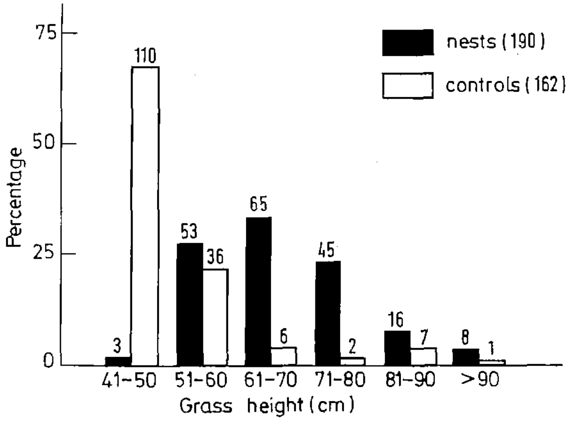

Fig. 7. Grass heights (posthatch period) at nest and control sites. The *n* of each group is given at the top of the columns

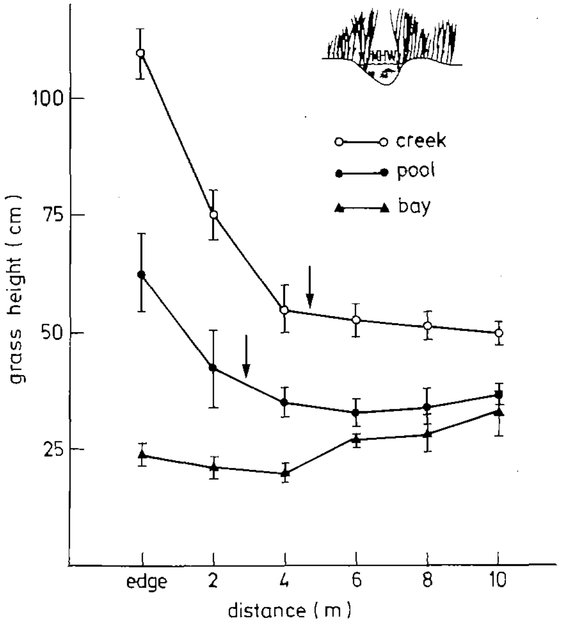

Fig. 8. *Spartina alterniflora* height (±SE) measured in the posthatch period as a function of distance from creeks, pools, and a bay. Arrows on creek and pool distributions indicate approximate average distances of nests from these bodies. Inset = schematic diagram of the relationship among grass height, ground elevation, and distance from creek edge

negatively correlated ($r = -0.30$, $df = 92$, $r = 0.50$, $df = 93$, $Ps < 0.001$, respectively). Nests near creeks were in significantly taller grass. (Table 2B) *and* on significantly lower ground than nests by pools (10.3 ± 0.3 vs. 12.6 ± 0.2 cm above MHW; $t = 2.73$, $df = 117$, $P < 0.01$). Grass height decreased as a function of distance from water and at equivalent distances was taller by creeks than by pools (Fig. 8). While patterns of grass height were comparable in the two study

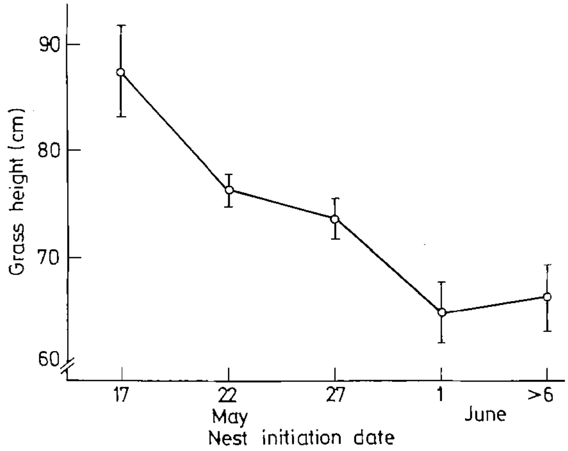

Fig. 9. Grass height (posthatch period) at nest as a function of the date of nest initiation

areas as indicated by the similar average grass heights at central and peripheral control sites (Table 2C), central pairs nested in significantly taller grass than pairs in the peripheral area (Table 2D). Gulls did not nest in the tallest grass on the water's edge (Fig. 8).

Throughout the season gulls consistently initiated nest building in grass about 35 cm in height. Grass at early nests had grown substantially by the time many later pairs nested, and thus after the seasonal surge of grass growth (cf. height at nest initiation and after hatching in Table 2), taller grass was associated with earlier nesting ($r = -0.30$, $df = 173$, $P < 0.001$; Fig. 9). Grass height, ground elevation, and proximity to water are interdependent features of nest sites and highly significant proportions of the variation in any one factor can be explained by multiple correlation of the others (R^2s ranging from 0.19 to 0.43; all Ps < 0.001).

2. *Tidal Flooding and Nesting Success*

From 1965 to 1974, seven floods in 5 years produced heavy reproductive losses in the colony (Table 3); two severe floods also occurred during 1975–77 (Andrews, personal communication). Floods early in the season, when grass is short, often destroy a greater proportion of nests than do later floods. Yet because pairs have sufficient time to renest after an early flood, these inundations are of less serious reproductive consequence than late ones. For instance, a flood in May 1972 destroyed 80% of the nests in the study areas but had much less impact on breeding success than did a flood in late June 1974, which destroyed 70% of the nests (Table 4). Only a small proportion of the breeding females had laid full clutches prior to the former flood, while very few relaid following the latter. Flooding toward the end of the nesting cycle or the occurrence of two floods in a single season resulted in the gulls' poorest production years (e.g., 1967, 1968, 1974; see Table 3).

Table 3. Wind and tidal characteristics of flooding that produced heavy reproductive losses in the gullery

Date[a]	FMI[b]	Tides (m)				Winds (km/h)			% nest loss
		Highest	Monthly $\bar{x}$	Max. speed	$\bar{x}$ speed	Monthly $\bar{x}$ speed	Direction	Monthly-direction	
15-16/6/65	0.99	3.08	2.69	38.6	29.4	17.5	60°	240°	90[d]
24/5/67	1.00	3.44	2.71	40.2	27.3	17.2	50°	280°	90[e]
18-19/6/67	0.87	2.84	2.66	61.1	NA	NA	40°	NA	90[e]
27-28/5/68	0.00	3.26	2.71	40.2	34.7	17.2	80°	240°	90[f]
9-10/6/68	0.95	3.41	2.74	28.9	14.6	15.2	130°	220°	90[f]
25-26/5/72	0.91	3.12	2.75	46.6	30.2	19.3	60°	140°	80[g]
22/6/72 (Agnes)	0.80	NA[c]	NA	49.8	35.8	7.0	280°	210°	0[g]
24-25/6/74	0.20	3.13	2.82	25.7	14.3	15.6	40°	140°	70[g]

[a] No flooding occurred during 1966, 1969, 1970, 1971, 1973

[b] Fraction moon illumination

[c] Not available

[d] Bongiorno (1970)

[e] Segré (1969)

[f] Chernesky (unpublished data); Impekoven (unpublished data)

[g] Present study

Table 4. Average (±SE) egg measurements, clutch sizes, and laying dates of laughing gulls in central and peripheral study areas during 1972-1974

Egg character	Central pairs	Peripheral pairs	t	df	$P<$
Length	53.6±0.1 cm	54.1±0.2 cm	1.80	714	0.10
Breadth	38.5±0.1 cm	38.1±0.1 cm	3.18	714	0.01
Shape index (L/B)	1.39±0.003	1.42±0.006	4.08	714	0.001
Volume	39.7±0.2 cc	39.1±0.3 cc	1.86	714	0.10
Laying date	12.2±0.4	15.3±0.5	4.57	549	0.001
Clutch size	2.51±0.03 (Mode=3)	2.21±0.05 (Mode=2)	$x^2=31.95$	2	0.001

Severe flooding occurred during spring tides, accompanied by sustained, onshore, NE winds (Table 3). The fraction of moon illumination (FMI) recordings were clustered around new (0.00) and full (1.00) moon phases, and tidal heights during floods (3.1 ± 0.1 m) averaged 0.6 m higher than the grand means of respective monthly MHW levels (see also Bongiorno and Swinebroad, 1969; Andrews, 1977). Winds were substantially stronger during flooding (25.1 ± 3.5 km/h) than average (17.1 ± 0.6 km/h) and blew from the NE (65.7 ± 11.9°) opposite mean wind direction from the SW (210.0 ± 3.5°). SW winds are buffered by the mainland before reaching the gullery and oppose incoming tides, whereas onshore winds sweep into the marsh and augment rising tides. Hurricane Agnes blew out of the SW and consequently produced only partial losses of three clutches.

On 24–25 June 1974, 88 of 125 (70%) nests in the study areas were destroyed by flooding, and very few females relaid; 63% of the nests (134/214) of areas I and II on Ring Island (60 km south of Brigantine) were also destroyed. Following this flood, the site features of nests of successful and unsuccessful pairs were compared.

As anticipated, pairs that nested on mats and in tall grass on low ground near creeks were more successful than pairs nesting at other sites; 47% (15/32) of nests on mats versus 22% (20/93) off mats survived the flooding ($\chi^2=6.39$, $df=1$, $P<0.02$). Grass height was significantly taller on average at successful (47.2 ± 2.0 cm) than at unsuccessful nests (39.4 ± 0.8 cm; $t=4.31$, $df=114$, $P<0.001$); this also held for grass on the SW sides of successful (49.0 ± 2.0 cm) and unsuccessful nests (41.7 ± 1.0 cm; $t=3.80$, $df=114$, $P<0.001$). Nesting success was significantly correlated with grass height around nests at nest initiation ($r=0.40$, $df=83$, $P<0.01$) and after hatching ($r=0.29$, $df=93$, $P<0.01$). Successful nests were, on average, built on significantly lower ground (7.8 ± 0.3 cm above MHW) than were unsuccessful nests (11.5 ± 0.3 cm; $t=2.56$, $df=119$; $P<0.05$); success and ground elevation were significantly negatively correlated ($r=-0.26$, $df=104$, $P<0.01$). Proportionally more nests near creeks (35/85) than nests near pools (2/40) survived the flood ($\chi^2=15.39$, $df=1$, $P=<0.001$); 40% (35/88) of the nests in the central area survived, while only 5% (2/37) of the nests in the peripheral area survived ($\chi^2=15.93$, $df=1$, $P<0.001$). The proportions of nests by creeks and nests by pools were not different between the central and peripheral areas in 1974.

A multiple linear regression between success and habitat measurements including nest height and inter-nest distance was not statistically significant ($R=0.55$, $F=1.50$, $df=12/40$), due apparently to the large number of predictors and corresponding small sample size. Grass height (at nest initiation) was the only statistically significant predictor of success ($t=2.38$, $df=40$, $P<0.05$). Grass measurements (at nest initiation and after hatching) combined to yield a significant regression with success ($R=0.46$, $F=7.08$, $df=3/81$, $P<0.005$); and grass height (at nest initiation) was the only single significant predictor of survival ($t=3.18$, $df=81$, $P<0.01$).

Discussion

1. Nest Site Selection

Laughing gulls selected nest sites that appeared to enhance the probability of eggs and chicks surviving flood tides. The gulls' attraction to mats has been previously demonstrated by Bongiorno (1970) who rearranged grass cuttings before laying and showed that pairs nested on accumulated debris. Mats, like nests, are buoyant and probably add stability to floating nests (see also Klopfer and Hailman, 1965). There is apparently a greater premium for nesting on mats for pairs in low marsh areas; the negative association between nest proximity to mats and to water indirectly supports this suggestion. Almost all pairs in a low marsh region of Ring Island nested on mats, whereas fewer than half of the pairs in a high marsh region did so.

Burger and Beer (1975) contended that mats were not desirable nesting sites because of difficulties involved with defending territories against nest material gatherers. While added vigilance and defense may be required of pairs nesting on mats (especially large mats), these potential costs appear to be more than offset by other benefits, as shown by the significant proportion of laughing gulls that selected nest sites on mats. Laughing gulls breeding on higher and drier ground than salt-marsh do not seem to nest near vegetational debris (Bent, 1921; Dinsmore and Schreiber, 1974).

The gulls showed no seasonal trend in their tendency to nest on mats, and the rafts of dead *Spartina* grasses were not a limiting factor for nesting. Yet the abundance and perhaps concentration of this material in an area may have had a significant influence on the gulls' tendency to nest on mats. On Ring Island, significantly more nests were on mats than in nesting areas in Brigantine, where there seemed to be less and more dispersed debris and where many mats were unoccupied. Moreover, nesting on mats and near neighbors were interrelated matters on Ring Island, where nesting density was significantly greater than in Brigantine. The tendency of unsettled pairs to nest near established pairs (see also Koskomies, 1957; Klopfer and Hailman, 1965; McNicholl, 1975b; Veen, 1977; Montevecchi et al., 1978) could attract nesting pairs to mats in these circumstances.

By nesting on a mat, a pair might also minimize energy expenditure in the collection of nest material (Klopfer and Hailman, 1965). Laughing gulls in the salt-marsh build elaborate nests (Chernesky et al., 1975), but perform virtually no building prior to egg aying. Laying an egg on or near the material of which the nest is to be built may also be adaptive in minimizing the exposure of freshly laid eggs to avian predators whose activity and success are greatest during the laying period (Beer, 1966; Montevecchi, 1977). Forster's (*Sterna fosteri*) and common terns (*Sterna hirundo* -Storey, 1978) and oyster catchers (*Haematopus palliatus*) nesting in salt marshes also nest on mats, as do many ground nesters in freshwater marshes (e.g., black terns *Chlidonias n. nigra* --Baggerman et al., 1956; Weller and Spatcher, 1965; Forster's terns and American coots *Fulica a. americana* --McNicholl, 1975a; pied-billed grebes *Posilymbus p. podiceps* --Weller and Spatcher, 1965).

Noble and Wurm (1943) had previously noted the laughing gulls' tendency to nest along tidal creeks. In the present study, laughing gulls were found to select nest sites by creeks *and* by pools, and while edge area was not a limiting factor (much edge area was unoccupied and the gulls showed no seasonal trends in tendencies to nest by water), the proportion of nests by creeks and by pools appeared to reflect the proportions of these types of edges in the study areas. There are many fewer pools in the dense laughing gull nesting areas (Ring Island) in Stone Harbor where Noble and Wurm (1943) worked, and this factor may account for gulls there not nesting by pools or for such a tendency to be overlooked by earlier workers. Ground nesting marsh birds usually nest near open water (e.g., Franklin's gull *Larus pipixcan* --Burger, 1974; black-headed gull *Larus ridibundus* -Ytreberg, 1956; clapper rail *Rallus longirostris*--Kozicky and Schmidt, 1949; Stewart, 1951; Johnson, 1973; cf. Andrews, 1977; old-squaw *Clangula hyemalis* -Evans, 1970). Burger (1974) has argued that nesting near open water may be adaptive for Franklin's gulls by (1) facilitating rapid escape from mammalian predators and (2) minimizing the chances of entanglement in vegetation. As the gullery in Brigantine is not accessible to terrestrial predators (Montevecchi, 1977) and as marsh grass is much more pliable than the cattails of the freshwater marshes where Franklin's gulls nest, neither of Burger's considerations appear applicable to laughing gulls. Rather, the most important factor attracting laughing gulls to nest near water is probably a proximate one, i.e., the gull's tendency to select nest sites in tall grass (see Fig. 8, see below; cf. Andrews, 1977). Tidal currents and substrate wetness may prevent gulls from nesting as near to creeks as to pools.

Laughing gulls nested on low ground just above average high tide levels and appeared to randomly select ground elevations on which to nest. This findings appears at variance with other reports that the gulls nest on high ground in the marsh (Noble and Wurm, 1943; Bongiorno, 1970; Burger and Shisler, 1978). Andrews (personal communication) has found that laughing gulls on lower marsh than the present study areas do nest on higher elevations than expected by chance. Interestingly, the densest nesting areas in Stone Harbor where Noble and Wurm (1943) and Bongiorno (1970) worked and the area on Clam Island where Burger and Shisler (1978) worked appear to be lower marsh than the present study area. Therefore, it appears that laughing gulls select higher (than random) sites on which to nest in low marsh habitat, but do not select higher elevations when nesting on higher marsh (see also Andrews, 1977). Nesting on low ground elevations is apparently a consequence of the gull's selecting nest sites in tall grass (see below; see Andrews, 1977). *Spartina alterniflora* growth is related to the time plants are inundated, taller plants growing on lower ground (Stewart, 1951; Ferringo, 1960; Teal and Teal, 1969; Andrews, 1977; see inset Fig. 8).

Throughout the season, gulls in the areas under study selected nest sites in grass about 35 cm in height, and as a result earlier nest initiation dates were associated with taller grass around the nest in the posthatch period. As larids tend to nest earlier with age (Austin, 1945; Ytreberg, 1956; Coulson and White, 1956, 1958, 1960, 1961; Coulson, 1966; Mills, 1973; Harrington, 1974; Ryder, 1975), it is feasible that older gulls might select nest sites with greater potential grass growth as a simple consequence of nesting earlier in the season. As will be discussed in the next section, tall grass holds nests in place during flooding, preventing them from being washed away by rising waters (Fig. 10). There are other apparent advantages associated with early nesting in the salt marsh. Relaying following the loss of eggs or chicks provides an important reproductive assurance for birds breeding in risky habitats. Gulls relay within 10–14 days, but because the probability of relaying decreases as the season progresses (e.g., Paludan, 1951; Segré, 1969; Bongiorno, 1970), it is probably advantageous to nest as early in the season as possible to insure that a second nesting attempt will be possible should it be needed (Andrews, 1977). Forster's terns possess some of the most elaborate of these adaptations for marsh breeding: they lay earlier than congeneric marsh nesters, relay more quickly than other larids, and, in contrast to other larids, show no reduction in clutch size in second layings (Storey, 1978).

Taller grass later in the season probably affords greater nest protection against flooding (Andrews, 1977; Storey, 1978) and also protects the semiprecocial gull chicks that wander from nests soon after hatching from avian predators, neighboring adults, intense solar radiation, and other climatic abuse (see also Bartholomew and Dawson, 1952; Tinbergen, 1953; Dawson et al., 1972). Tall dense grass around nests may also favor the chicks' capacity to learn to recognize the calls of parents (Beer, 1969; Impekoven and Gold, 1973; see also Evans, 1977). The reduction of visibility of nesting neighbors may provide a mechanism that helps to insure that pairs nest in tall grass (Burger, 1977).

It appears that in order to nest in tall grass the gulls have to 'trade off' other nest site features, such as ground elevation and distance to open water, which might also provide useful nest protection during flooding. These 'trade offs' also increase the likelihood of nests being wet (see also Andrews, 1977). Laughing gulls nesting in other areas of the salt marsh and in other habitats select nest sites that involve other sorts of 'trade offs.'

Like some other larids nesting in ephemeral habitats (Kirkman, 1937; McNicholl, 1971; Burger, 1974; Storey, 1978), laughing gulls arrive at and occupy breeding grounds well before (4–5 weeks) egg laying (Segré, 1969; Bongiorno, 1970; Dinsmore and Schreiber, 1974). Because the gulls engage in extremely little nest building before egg laying, nest site selection activities could occur throughout the extended prelaying period during which time gulls are exposed to two spring tides (new and full moon) on the breeding grounds. Spring tides restrict roosting areas and may provide important information about nest site suitability (see also Bongiorno, 1970; Andrews, 1977; Storey, 1978). The absence of pre-egg nest construction conserves energy during a period when the gulls' fitness apparently benefits more from mobility than site attachment on the breeding grounds, possibly allowing more time to select 'safe' sites. Clapper rails nesting in the salt marsh may employ a similar strategy (Andrews, 1977).

2. *Tidal Flooding and Nesting Success*

The specificity of climatic conditions that cause flooding, the frequent occurrence of flooding, and its drastic impact on reproductivity combine to impose a strong, directional selection on the gulls' nesting strategies. Tall grass associated with low ground elevations (not the lowest) just above average high tidal levels along creeks held floating nests in place during flooding. Many successful nests were tipped up against tall grass along the SW sides of nests. Nests on mats had more edge that could be fenced in by and entangled in emergent grass. Because severe floods are accompanied by NE winds, it appears that on low marsh elevations pairs nesting in tall grass or with tall grass on the SW side of the nest will be more fit than pairs nesting elsewhere. Present findings support and extend those of Bongiorno (1970). As an adaptation to NE storms, winds, and tidal forces, Forster's terns do not nest in salt marsh areas with northeastern exposures on open water and nest in the interior of large islands and on the southwestern and western sides of small islands (Storey, 1978). Laughing gulls employ alternative nesting strategies when breeding in other areas of the marsh, e.g., high ground (Bent, 1921; Chernesky et al., 1975), but the findings reported here can probably be generalized to other laughing gulls nesting on low marsh habitat.

Nest loss due to flooding was greater on the low ground area of Ring Island, whereas it was greater on the higher ground area (peripheral) in Brigantine. The flood completely covered both study areas in Brigantine, but did not appear to entirely inundate the high ground area on Ring Island. These outcomes support the suggestion that during floods that inundate the entire marsh success will be greatest among nesters on lower ground but that during floods that do not inundate the entire colony success will be greatest among nesters on higher ground (Chernesky, in litt.). Storey (1978) has presented similar evidence for colonies of common terms. The former type of flood carries the most severe consequences for the population, while the latter claims fewer nests but occurs more often.

Flooding destroyed proportionally fewer nests in the central area than in the peripheral area. The greater success of the pairs in the central area was attributed to (1) their tendency to nest in taller grass than peripheral pairs and (2) the greater protection of the central area from tidal forces (see also Storey, 1978). Among colonial birds, central nesters are often the most successful members of the colony (Patterson, 1965; Coulson, 1968; Tenaza, 1971; Dexheimer and Southern, 1974; Coulson and Horobin, 1976; Parsons, 1976; Hutson, 1977).

Only about 30% of the variance in nesting success was accounted for by the variables studied. Other factors may be more crucial for nesting success during flooding than those studied. Different floods may impose different pressures on the nesting gulls and the multiple pressures that select adaptive nest sites may interact such that only a small (though biologically significant) amount of the variance in nesting success can be explained at a single point in time (see also Storey, 1978).

Subtle age (experience) related changes in nest site preferences and/or in nest construction may be important. Egg size is a valid and reliable index of female age class in larids and other birds; females tend to lay smaller, more elongated eggs during initial breeding attempts (Romanoff and Romanoff, 1949; Andersen, 1957; Coulson, 1963; Coulson et al., 1969; Ryder, 1975). Female larids breeding for the first time also tend to lay later in the season (references above) and to lay smaller clutches (Coulson and White, 1958, 1961; Klomp, 1970; Mills, 1973; Ryder, 1975; cf. Parsons, 1975). No significant differences were found between the average egg sizes, clutch sizes, or laying dates of successful and unsuccessful nesters. However, only a few eggs in peripheral nests were measured during 1974 (three complete clutches), so the egg size analysis was essentially a comparison among pairs in the central area. When egg sizes, clutch sizes, and dates of laying onset were compared over 3 years, each attribute consistently indicated that younger females (and probably pairs, as younger males tend to mate with younger females -Coulson and White, 1958, 1961; Mills, 1973) tended to nest in the peripheral area of the colony (Table 4). On the basis of this indirect evidence, it is suggested that younger pairs will during flooding be at a selective disadvantage to older pairs as a consequence of nesting in suboptimal habitat.

Young Arctiv terns (*Sterna paradisaea*) often nest in less suitable sites than do older pairs (Coulson and Horobin, 1976), and Van Bree (1957) found that black-headed gulls nesting in a vulnerable low area in a salt-marsh laid smaller eggs than did pairs on higher marsh. Evidence from many other colonial species also indicates that older birds tend to nest centrally or in optimal regions in the colony (Coulson, 1963, 1968; Nelson, 1967; Cooke and Finney, 1973; Ludwig, 1974; Ryder, 1975; Blus and Keahey, 1978).

The earlier arrival of older pairs could allow them initial access to preferred areas from where they might repel later, younger arrivals. But the sparse nesting density of the gullery seems to indicate that many more pairs could nest in any area of the colony (see also Hutson, 1977). The suggestion that the nesting area of the colony might be partitioned in an age-dependent manner raises many such questions, which can only be investigated by long-term, collaborative programs that include banding large segments of the population; a program of this nature is ongoing (Andrews et al., 1977).

Breeding experience enhances behavioral and reproductive efficiency (e.g., Lehrman, 1961; Coulson, 1966), but little direct evidence is available on the effects of nesting experience on breeding success and fitness. Bongiorno (1970) found that many laughing gulls relaid in an area 2 weeks after a flood had devastated nests there. The peripheral area in Brigantine where 95% of the nests were destroyed late in the 1974 season was populated by an equal number of nesting pairs in 1975. It is not known, however, whether gulls renesting in such areas select safer sites and/or build better nests. Some nesting groups of laughing gulls have been known to abandon unsuccessful areas following a flood and to nest in previously uninhabited areas (M. Impekoven, personal communication; Klopfer and Hailman, 1965; see also Hardy, 1957; Beer, 1966; Storey, 1978; Pinkowski, 1978).

By making less than a full physiological commitment to reproduction (laying smaller clutches of smaller eggs), especially during initial breeding attempts, younger birds may conserve energy in a phase of the life cycle when they are trying new behavioral adjustments and the probability of nesting in less than optimal habitat is high (see also Lack, 1968). Behavioral competence, nest site suitability, reproductive investment, and fitness appear to improve concurrently with age.

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