# COLONY SITE DYNAMICS AND HABITAT USE IN ATLANTIC COAST SEABIRDS

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ABSTRACT.—Seabird colony sizes and movements were documented in the DelMarVa coastal region in 1976–1977 and in New Jersey in 1978–1979. Most colonies were found on marsh and dredge deposition islands and on barrier island beaches. For the "traditionally" beach-nesting Herring Gull, Common Tern, and Black Skimmer, larger, more stable colonies were found on barrier beaches than on marsh islands. In marsh habitats, rates of colony-site change of marsh-nesting Forster's Tern and Laughing Gulls were similar to those of the former beach nesters. Several adaptations have evolved in marsh specialists to cope with a high risk of reproductive failure due to flooding, but both Herring Gulls and Common Terns also appear to be very adaptable in nesting under various habitat conditions.

New colonies and those abandoned between years may be pioneering attempts by younger or inexperienced birds, because they are often smaller than persistent colonies, although patterns differ among areas and habitats. Colony-site dynamics are complex and result from many selective factors including competition, predation, physical changes in site structure, and flooding. The invasion of Herring Gulls into marshes along the mid-Atlantic coast has had an impact on new colony-site choice by associated seabirds.

Calculating colony-site turnover rates allows for comparisons among species, habitats, and regions and may give useful insights into habitat quality and change and alternative nesting strategies. *Received 10 November 1980, accepted 20 February 1981.*

COLLECTIVELY, colonially nesting seabirds (here referring to gulls, terns, and Black Skimmers, *Rynchops niger*) nest in a variety of habitats along the North and mid-Atlantic coast, including beaches and dunes, salt marshes, dredge deposition islands, rocks, etc. (Bent 1921, Stone 1937, Erwin 1979a). Some species are habitat specialists. Forster's Terns (*Sterna forsteri*) and Laughing Gulls (*Larus atricilla*), for instance, nest nearly exclusively in salt marshes in the mid-Atlantic coastal region (Montevecchi 1978, Storey 1978, Erwin and Korschgen 1979). Others such as Common Terns (*Sterna hirundo*) and Herring Gulls (*Larus argentatus*) nest in several different habitat types ranging from marshes to rocky islands (Burger 1977, Burger and Lesser 1978, Erwin 1980).

Recently, many North and mid-Atlantic coast colonies of Herring Gulls, Common Terns, and Black Skimmers have shifted from their traditional (Bent 1921, Stone 1937) outer beach-dune habitats to salt marshes and bay islands, due largely to human disturbances along beaches (Buckley and Buckley 1977, in press; Burger 1977; Burger and Lesser 1978; Erwin 1980). Recent coastal surveys (Erwin 1979a, Erwin and Korschgen 1979, Parnell and Soots 1980, Buckley and Buckley in press) showed that in the states with the greatest coastal zone development, the use of marsh and dredge deposition islands by traditional "beach nesters" is highest.

Major changes in breeding habitat use patterns pose a number of ecological and evolutionary challenges to the individual organism. More specifically for nesting seabirds, the major factors affecting the relative fitness of the individual in different habitats include the risk of flooding of eggs or young (Greenhalgh 1974, Montevecchi 1978, Burger 1979a, Burger and Lesser 1979), the physical stability of sand, marsh, and rocky substrates (McNicholl 1975, Southern 1977), predation (Buckley and Buckley 1972, Burger 1979b, Burger and Lesser 1978), and competition for nest sites (Crowell and Crowell 1946; Nisbet 1971, 1973; Burger and Shisler 1978; Erwin 1980).

For ground-nesting seabirds in disturbed areas, the shift from use of open, dry dune- and beach-sand substrates to the more vegetated wet marshes of lower elevation represents an abrupt change; both Common Terns and Herring Gulls, however, have demonstrated sufficient plasticity to make at least one important adjustment—nest building behavior (Burger 1979a). Other species, such as Black Skimmers, may not be quite as "plastic," as they are nearly exclusively sand nesters. In addition to the change in the physical regime of the nesting site, the biotic environment might also change with more intense competitive and predatory interactions occurring as the amount of occupiable habitat becomes limiting. Large, aggressive Herring Gulls usurp nest sites by breeding earlier than most other species and also prey on the young of other species (Hatch 1970, Burger 1977, Burger and Lesser 1978). Both Common Terns (Burger and Lesser 1978, 1979; Erwin 1980; see Nisbet 1973 and Drury 1973, 1974 for historical review) and Laughing Gulls (Nisbet 1971; Burger 1977, 1979a; Burger and Shisler 1978) have been shown to be adversely affected by the presence of nesting Herring Gulls.

Ultimately, the ability of each species to cope with these changes should be reflected in the reproductive output of the individuals affected. Low reproductive success in seabirds is often associated with declining colony size or abandonment of colony sites (Crowell and Crowell 1946, Morris and Hunter 1976, Burger unpubl. data). Because these habitat shifts have occurred mostly in the past 30–50 yr (Stone 1937, Buckley and Buckley 1977, Burger 1977, Erwin 1980), we would expect selection still to be acting rather strongly (a nonequilibrium condition).

We propose here to compare the dynamics of colony-site use and colony sizes among five seabird species in New Jersey, a region of intense coastal development, with that on the Delaware-Maryland-Virginia (hereafter DelMarVa) coast, an area comprised largely of undisturbed barrier islands (Erwin 1980). In New Jersey, virtually all nesting of the five species is on salt marsh islands or dredge deposition islands, while in Virginia Herring Gulls, Common Terns, and Black Skimmers still nest primarily on barrier island beaches and dunes under relatively pristine conditions (Erwin 1980).

Given the above scenario, we pose the following questions: (1) Are beach-dune colonies of the "traditional beach" nesters any different in size or stability from year to year than those colonies in marshes or on dredge islands? (2) Are colonies of the marsh-adapted species, i.e. Forster's Tern and Laughing Gull, more consistent in site use from year to year than the marsh "invaders?" Presumably, the latter species have not had sufficient time to acquire fine-tuned adaptations and, hence, are possibly inferior in judging high quality sites in marshes. (3) Do new colonies or colonies abandoned between years differ in any way from those that persist? (4) How does the presence of the competitively dominant and predatory Herring Gull influence the colony-site choice of other species?

We respond to these questions by examining comprehensive census data collected since 1976.

## METHODS

Surveys and censuses of nesting colonies were conducted in late May and June in 1976 and 1977 along the Delaware-Maryland-Virginia coast from Cape Henlopen, Delaware to Cape Charles, Virginia (hereafter called "DelMarVa") using helicopter, fixed-wing aircraft, and ground methods (see Erwin 1979a for details). Similarly, in New Jersey, waterbird surveys have been conducted annually since 1976 through joint State, Federal, and private efforts (Kane and Farrar 1976, 1977; Galli 1978, 1979; Erwin 1979a).

Colony locations were recorded on U.S. Geological Survey maps, and census figures for each breeding species were determined either by estimating the number of adults in the colony (aerial survey) or by counting all nests with eggs and then multiplying by 2 to obtain the total breeding adult estimate. In most cases, the same observers censused the same colonies in consecutive years to allow for meaningful comparisons. Two pairs of birds or more were considered to define a "colony." Because we were interested in colony-site dynamics, a colony abandonment was recorded whenever a location was occupied one year but not the next. As there is no consensus in defining a colony's spatial limits (Buckley and Buckley 1979), an arbitrary distance of 200 m was established as the minimum distance required for a colony movement. New colonies were those established in a given year that were at least 200 m from a formerly occupied site.

One method of assessing colony-site dynamics is to calculate colony turnover rates (Erwin 1977):

$$T = \frac{1}{2}\left(\frac{S_1}{N_1} + \frac{S_2}{N_2}\right)$$

where $S_1$ = number of sites occupied only at first census; $N_1$ = total number of sites, first census; $S_2$ = number of sites occupied only at second census; $N_2$ = total number of sites, second census; and $T$ is expressed as an annual rate (note $T_{max} = 1.0$ where $T$ can then be converted to a percentage).

We concentrate here on the following five species: Herring Gull, Laughing Gull, Common Tern, Forster's Tern, and Black Skimmer. Emphasis is placed on barrier beach and dredge and marsh islands as colony sites. In only a few cases are other habitat types such as mainland beach or roadside construction fill used. Because these other habitats contained less than 1% of the total of a given species, they were not included in the analysis.

Colony-site occupation in 1976 and 1977 in the DelMarVa region and in 1978 and 1979 in New Jersey is examined. The 1976 and 1977 New Jersey surveys were conducted differently than the 1978–1979 surveys and therefore were not included here. In New Jersey, both the numbers of colonies and total bird numbers showed an increase in the coastal surveys from 1976 to 1978 (Kane and Farrar 1976, 1977; Galli 1978, 1979), probably reflecting improved efficiency in surveying rather than true population increases in most cases.

For colony-size comparisons, nonparametric Mann-Whitney $U$ tests are used (with $Z$ values given for large samples), but tables show both medians and means with standard deviations.

## RESULTS

### COLONY SIZES

*Habitat differences.*—Overall species nesting data for the two regions are shown in Table 1. Colony sizes varied considerably for most species between years in both New Jersey and DelMarVa (Tables 2 through 6). The only species to show a substantial population change in the DelMarVa area was the Herring Gull, which doubled in numbers from 1976 to 1977 (Erwin 1979a), with a concomitant increase in mean colony size (Table 3). Herring Gulls decreased by about 30% in New Jersey and were distributed in more numerous, smaller colonies the second year. Forster's Terns, in both regions, were the most consistent in colony size in successive years (Table 4).

Differences in colony size were found between habitats for all species. Mean colony sizes of Herring Gulls were larger on barrier islands in DelMarVa in both 1976 and 1977 than those on marsh islands, but sample sizes were too small to detect

TABLE 1. Recent population estimates of breeding seabirds along the New Jersey and DelMarVa coasts.[a]

| Species | Area | Population estimate[b] (adults) |
|---|---|---|
| Laughing Gull | New Jersey | 53,387 |
| | DelMarVa | 32,926 |
| Herring Gull | New Jersey | 5,839 |
| | DelMarVa | 3,180 |
| Common Tern | New Jersey | 9,518 |
| | DelMarVa | 8,600 |
| Forster's Tern | New Jersey | 1,167 |
| | DelMarVa | 2,450 |
| Black Skimmer | New Jersey | 1,803 |
| | DelMarVa | 5,700 |

[a] New Jersey includes area from Cape May to Sandy Hook; DelMarVa includes area from Cape Henlopen, Delaware to Cape Charles, Virginia along the ocean coast and on the Chesapeake Bay from Somerset County, Maryland south to Cape Charles.
[b] Most current estimates reported in New Jersey from 1979, DelMarVa from 1977.

a significant difference in the medians (for 1976 data, Mann-Whitney $U = 16$, $P = 0.44$). In New Jersey, no detectable statistical differences were found in the sizes of marsh and dredge island colonies (1978, $Z = -0.93$, $P = 0.36$; 1979, $Z = -0.03$, $P = 0.98$, two-tailed tests).

Both Common Terns and Black Skimmers, frequent colony associates (Gochfeld 1978, Erwin 1979b), had much larger colonies on barrier island beaches than on marsh islands in DelMarVa (Tables 5 and 6). The magnitude of the difference in Common Terns was more marked in 1976 ($U = 21$, $P = 0.01$, one-tailed) than in 1977 ($U = 76$, $P > 0.05$). The differences in Black Skimmer colony sizes between habitats was so striking that no statistical test was necessary. In New Jersey, Black Skimmer colonies on dredge islands were substantially larger than those on marshes. Comparing regions, marsh colonies of Common Terns were larger in DelMarVa than in New Jersey ($Z = -3.11$, $P < 0.01$, two-tailed), while Black Skimmers showed the opposite pattern. Black Skimmers formed very large colonies on dredge islands in New Jersey, although these were limited in number.

*New and abandoned colonies.*—Although sample sizes were often small, new colonies and those abandoned between years were generally smaller in size than the overall average for most species and habitats. For Laughing Gulls, new colonies

TABLE 2. Colony-site dynamics in Laughing Gull marsh habitats.

| Area | Year | Colony size[a] | | $n$ |
|---|---|---|---|---|
| | | $\bar{x} \pm$ SD | Median | |
| DelMarVa | 1976 | 722 ± 735 | 450 | 20 |
| | Deserted (1976–1977) | 721 ± 907 | 721 | 2 |
| | 1977 | 1,037 ± 1,131 | 576 | 25 |
| | New | 567 ± 366 | 576 | 7 |
| | | | | $T = 0.19$[b] |
| New Jersey | 1978 | 863 ± 2,122 | 120 | 51 |
| | Deserted (1978–1979) | 1,155 ± 2,485 | 60 | 5 |
| | 1979 | 461 ± 1,092 | 70 | 66 |
| | New | 68 ± 181 | 20 | 20 |
| | | | | $T = 0.20$[b] |

[a] Number of adults in colony.
[b] Turnover rate (see text for formula).

TABLE 3. Colony-site dynamics in Herring Gulls.

| Area | Habitat | Year | Colony size | | $n$ |
|---|---|---|---|---|---|
| | | | $\bar{x} \pm$ SD | Median | |
| DelMarVa | Marsh island | 1976 | 23 ± 33 | 25 | 9 |
| | | Deserted (1976–1977) | 0 | | |
| | | 1977 | 80 ± 98 | 27 | 14 |
| | | New | 11 ± 5 | 10 | 5 |
| | | | | | $T$ = 0.18[a] |
| | Barrier beach | 1976 | 194 ± 345 | 9 | 5 |
| | | Deserted (1976–1977) | 54 ± 83 | 9 | 3 |
| | | 1977 | 633 ± 873 | 633 | 2 |
| | | New | 0 | | |
| | | | | | $T$ = NA[a] |
| New Jersey | Marsh island | 1978 | 238 ± 582 | 50 | 30 |
| | | Deserted (1978–1979) | 3 ± 1 | 3 | 7 |
| | | 1979 | 121 ± 287 | 18 | 39 |
| | | New | 8 ± 17 | 3 | 16 |
| | | | | | $T$ = 0.32[a] |
| | Dredge island | 1978 | 116 ± 169 | 85 | 13 |
| | | Deserted (1978–1979) | 49 ± 64 | 49 | 2 |
| | | 1979 | 77 ± 81 | 63 | 16 |
| | | New | 7 ± 4 | 6 | 5 |
| | | | | | $T$ = 0.23[a] |

[a] Turnover rate.

were significantly smaller than the overall median in New Jersey ($Z = -1.84$, $P = 0.03$), but no detectable median differences were found in DelMarVa ($Z = -0.73$, $P = 0.23$) (Table 2), even though the mean of new colonies was only about half that of the overall mean.

Herring Gulls formed very small new colonies in both DelMarVa and New Jersey (Table 3). In DelMarVa, samples were too small to show significant differences ($U = 17$, $P > 0.05$, one-tailed), but in New Jersey the difference is obvious. Similarly, deserted colonies of gulls in both regions were very small.

Both deserted and new colonies of Forster's Terns were of the same size as the overall yearly medians in DelMarVa ($Z = -1.06$, $P = 0.14$ and $Z = -0.47$, $P = 0.32$, respectively) (Table 4). In New Jersey, new colonies, although somewhat smaller than the overall colony size, were not significantly so ($Z = -1.36$, $P = 0.09$).

TABLE 4. Colony-site dynamics in Forster's Tern marsh habitats.

| Area | Year | Colony size | | $n$ |
|---|---|---|---|---|
| | | $\bar{x} \pm$ SD | Median | |
| DelMarVa | 1976 | 72 ± 63 | 54 | 21 |
| | Deserted (1976–1977) | 43 ± 29 | 40 | 9 |
| | 1977 | 58 ± 47 | 49 | 24 |
| | New | 48 ± 38 | 40 | 12 |
| | | | | $T$ = 0.47[a] |
| New Jersey | 1978 | 59 ± 91 | 33 | 16 |
| | Deserted (1978–1979) | 33 ± 18 | 35 | 3 |
| | 1979 | 50 ± 70 | 20 | 27 |
| | New | 23 ± 24 | 15 | 14 |
| | | | | $T$ = 0.36[a] |

[a] Turnover rate.

TABLE 5. Colony-site dynamics in Common Terns.

| Area | Habitat | Year | Colony size | | n |
|---|---|---|---|---|---|
| | | | $\bar{x}$ ± SD | Median | |
| DelMarVa | Marsh island | 1976 | 71 ± 75 | 40 | 9 |
| | | Deserted (1976–1977) | 35 ± 35 | 20 | 3 |
| | | 1977 | 120 ± 103 | 100 | 13 |
| | | New | 89 ± 68 | 100 | 7 |
| | | | | | $T = 0.44$[a] |
| | Barrier beach | 1976 | 239 ± 274 | 131 | 12 |
| | | Deserted (1976–1977) | (450) | — | 1 |
| | | 1977 | 211 ± 191 | 100 | 15 |
| | | New | 54 ± 46 | 54 | 4 |
| | | | | | $T = 0.18$[a] |
| New Jersey | Marsh island | 1978 | 100 ± 231 | 38 | 81 |
| | | Deserted (1978–1979) | 48 ± 81 | 18 | 10 |
| | | 1979 | 99 ± 237 | 40 | 99 |
| | | New | 30 ± 49 | 27 | 28 |
| | | | | | $T = 0.20$[a] |

[a] Turnover rate.

In DelMarVa, deserted colonies of Common Terns were only half the size of the overall average, but new colonies were not significantly smaller than the yearly medians ($U = 35$, $P > 0.05$). In New Jersey, however, both deserted ($Z = -1.92$, $P = 0.03$) and new ($Z = -1.77$, $P = 0.04$) colonies were smaller than the overall medians.

For Black Skimmers, small numbers of colonies in DelMarVa precluded statistical testing. In New Jersey, both deserted and new marsh colonies were much smaller than the overall colony size, although new colonies were not significantly different from the overall size ($Z = -0.41$, $P = 0.34$).

TABLE 6. Colony-site dynamics in Black Skimmers.

| Area | Habitat | Year | Colony size | | n |
|---|---|---|---|---|---|
| | | | $\bar{x}$ ± SD | Median | |
| DelMarVa | Marsh island | 1976 | 24 ± 20 | 14 | 5 |
| | | Deserted (1976–1977) | 23 ± 25 | 23 | 2 |
| | | 1977 | 19 ± 18 | 10 | 7 |
| | | New | 27 ± 22 | 23 | 4 |
| | | | | | $T = 0.49$[a] |
| | Barrier beach | 1976 | 195 ± 167 | 160 | 13 |
| | | Deserted (1976–1977) | 227 ± 315 | 227 | 2 |
| | | 1977 | 197 ± 155 | 120 | 13 |
| | | New | 213 ± 209 | 213 | 2 |
| | | | | | $T = 0.15$[a] |
| New Jersey | Marsh island | 1978 | 87 ± 181 | 27 | 12 |
| | | Deserted (1978–1979) | 21 ± 8 | 14 | 3 |
| | | 1979 | 112 ± 224 | 36 | 17 |
| | | New | 32 ± 56 | 4 | 8 |
| | | | | | $T = 0.36$[a] |
| | Dredge island | 1978 | 317 ± 296 | 295 | 4 |
| | | Deserted (1978–1979) | 70 ± 57 | 70 | 2 |
| | | 1979 | 483 ± 590 | 483 | 2 |
| | | New (1979) | 0 | | |
| | | | | | $T$ = NA[a] |

[a] Turnover rate.

TABLE 7. The influence of Herring Gull presence on colony-site abandonment and establishment by associated seabirds in marsh island colonies.

| Species | Area | Gulls present[a] | | Absent | $P^b$ |
|---|---|---|---|---|---|
| Common Tern | New Jersey | Abandoned | 4 | 6 | <0.01 |
| | | New | 0 | 28 | |
| | DelMarVa | Abandoned | 2 | 1 | ns |
| | | New | 0 | 7 | |
| Black Skimmer | New Jersey | Abandoned | 2 | 1 | ns |
| | | New | 0 | 8 | |
| | DelMarVa | Abandoned | 2 | 0 | ns |
| | | New | 0 | 4 | |
| Forster's Tern | New Jersey | Abandoned | 1 | 2 | ns |
| | | New[c] | 0 | 11 | |
| | DelMarVa | Abandoned | 3 | 6 | ns |
| | | New | 0 | 12 | |
| Laughing Gull | New Jersey | Abandoned | 3 | 2 | <0.01 |
| | | New[c] | 0 | 19 | |
| | DelMarVa | Abandoned | 0 | 2 | ns |
| | | New | 1 | 6 | |
| Total | | Abandoned | 17 | 20 | |
| | | New | 1 | 95 | <0.01 |

[a] Gull nesting at least partly overlapping with associated species.
[b] Based on Fisher Exact Probability Test, ns = not significant, $P > 0.05$.
[c] One colony not adequately mapped to determine precise nesting areas.

## Colony Site Turnover

In the DelMarVa region, site fidelity was highest for beach-nesting Common Terns (Table 5) and skimmers (Table 6) and marsh-nesting gulls (both species) (Tables 2 and 3) and lowest for marsh-nesting Forster's (Table 4) and Common terns and skimmers.

In New Jersey, the pattern was quite different. On marsh islands, Laughing Gull colony turnover (Table 2) was similar to DelMarVa but Common Terns (lower) (Table 5) and Herring Gulls (higher) (Table 3) had different colony turnover rates. Herring Gull colony use was more consistent on dredge islands than in marshes. Both Forster's Terns (Table 4) and skimmers (Table 6) had high turnover rates in marshes but not as high as in DelMarVa.

## Colony Desertion and Establishment—the Herring Gull Factor

We examined the influence of the predatory and competitively dominant Herring Gull nesting in marsh colonies on site abandonment and establishment for the other four species (Table 7). Because Herring Gull presence in either year 1 or year 2 could influence abandonment by the other species, the two years were combined in the table. New colonies, obviously, would only be influenced by gull presence in year 2. The overall pattern of colony establishment appears to be strongly influenced by gull presence in both regions, even though only two of eight comparisons were statistically different (Table 7). Small individual test samples probably explain this result.

# Discussion

The results above will be discussed in light of each of the questions posed in the Introduction.

## Colony Size and Stability of Traditional "Beach-dune Species"

The prediction that beach colonies are larger and more stable between years than marsh and/or dredge island colonies is only partially borne out by the results above. In DelMarVa, the colonies are larger and more stable on barrier islands than on marsh islands for all three species. Herring Gull nesting on barrier islands in the DelMarVa region is sparse and recent, beginning only about 10 yr ago during the southern expansion of the breeding range. The original coastal colony at Fisherman Island is still present and growing (Erwin 1979a).

In New Jersey, cross-habitat comparisons cannot be made, because barrier islands are essentially unused by breeding birds because of disturbance (Erwin 1980). Dredge islands are somewhat more stable than marsh sites for Herring Gulls. Because dredge deposition sites are higher (Buckley 1978) and may provide a sandy beach-like substrate, they may be more attractive to gulls and skimmers than the wetter, more flood-prone marsh habitats. The median size of dredge island colonies was larger than that for marsh colonies in both years (but not statistically different). Skimmer colonies are larger on the few dredge sites than either marsh or barrier island colonies.

New Jersey marsh colonies of skimmers seem to be fairly unstable, as in DelMarVa, but Common Tern marsh colonies are much more stable. A large difference in sample size precludes making a strong interpretation of this. New Jersey Common Terns are quite capable of adapting to wetter microhabitats (Burger 1979b). Perhaps marsh nesting has occurred for a longer period of time in New Jersey (Wilson 1854, Stone 1937, Burger and Lesser 1979), allowing the terns to adapt to this new situation. The New Jersey coast has a long history of recreational use, while the beach resort areas of DelMarVa are much more localized and more recent in their development. In Delaware, no marsh nesting by Common Terns or skimmers had been documented until 1976 (M. Byrd pers. comm., Erwin 1979a).

The small size of most marsh colonies of skimmers and Common Terns compared to colony sizes in "traditional" habitats in other areas (Portnoy 1977, Erwin 1979a) may in part be related to limited nesting substrate availability. Burger and Lesser (1978) found that both species confined most of their nesting to narrow, peripheral bands of drifted vegetation fragments (windrow or wrack), apparently avoiding the live *Spartina,* which covers the majority of the island area. It is unlikely that such strict physical limitations of this nature exist on most barrier or rocky islands (Bent 1921, Erwin 1979a, b). Of course, colony sizes are highly variable and are determined by a number of factors other than habitat space.

One likely cause of marsh colony abandonment is the high probability of flooding (Burger 1977; Burger and Lesser 1978, 1979; Montevecchi 1978; Storey 1978). Although barrier islands are subjected to storm flooding (Stone 1937, Burger and Lesser 1978), they provide greater relief than the flat marshes.

## Site Fidelity of Marsh vs. Non-marsh Species

The results do not seem to support the prediction that colony site change, i.e. turnover, should be lower for marsh specialists than "invader" species in marsh habitats. Although Laughing Gulls are somewhat more stable than marsh-nesting Herring Gulls in New Jersey, the two species are almost identical in colony turnover rate in DelMarVa marshes. Turnover rate comparisons must be interpreted cautiously here (Erwin 1977), however, because DelMarVa Herring Gulls are increasing markedly in numbers. Turnover rates of Forster's Tern colony sites are very high in both regions, on the same order as marsh-nesting Common Terns and skimmers. In fact, the rates are among the highest for all species in any habitat.

The contrast in site turnover between the two marsh-adapted species illustrates the need to examine species-specific microhabitat selection in some detail. Perhaps the gross habitat classification of marsh, dredge island, beach used here obscures the within-habitat heterogeneity that provides the real selective cutting edge.

Colony-site abandonment might be more readily understood by examining site selection and nest-building tactics. Even though Forster's Terns are strictly marsh nesters, they may not be superior to Common Terns or skimmers in judging safe sites or even in constructing more "flood-proof" nests. Bent (1921) claimed that Forster's Terns build large, elaborate (stable?) nests, but Storey (1978) contradicts this based on her work in Virginia and New Jersey. In recent, unpublished work, one of us (RME) has noted very little structural difference between Forster's and Common tern nests in either New Jersey or Maryland. Storey indicated that flooding was a major source of nest loss and that colonies did not reoccupy the same sites after washouts. One safe nest-siting strategy does not exist, because conditions change depending on a variety of wind and tidal combinations (Storey 1978).

Both Laughing Gulls and Forster's Terns have evolved certain adaptations that enhance nesting-success prospects *vis-a-vis* flooding danger. Laughing Gulls spend a lot of time in clubs "prospecting" for sites in the marsh during high Spring tide periods before energy is committed to nest building (Montevecchi 1978). Forster's Terns nest earlier than other terns and re-lay clutches quickly after storm washouts (Storey 1978). They also vary the size of the nest depending on the elevation of the substrate (McNicholl 1971). Both species select either buoyant substrate or elevated sites (e.g. muskrat houses by Forster's Terns) (Bongiorno 1970, McNicholl 1971). Certain formerly "non-marsh" species may, nonetheless, possess enough plasticity to adjust rapidly to these "new" nesting conditions. Herring Gulls and Common Terns both build larger nests in wet habitats than in dry, upland areas (Borodulina 1966 in Storey 1978, Burger 1977), and both show well-developed nest-repair behavior after flood damage (Burger 1979b).

## Desertion of Sites and New Colony Formation

*Size.*—Some seabird studies have found that certain colonies or certain parts of colonies are more successful than others (Coulson 1968, Drury and Nisbet 1972, Dexheimer and Southern 1974, Montevecchi 1978). Less suitable sites may be occupied predominantly by inexperienced and/or younger pairs (Coulson 1968, Ryder 1975, Blus and Keahey 1978) with high reproductive failure rates. One might expect that pioneering colonies in "new" habitats might be attempted by small numbers of younger individuals. Such "experiments" probably often lead to failure, but an occasional success may lead to range expansion or exploitation of new adaptive zones. Custer et al. (1980) found that abandoned and new "satellite" heron colonies were smaller than reused colonies.

The New Jersey data generally showed that new colonies and those abandoned between years were smaller than the persistent colonies. New and abandoned colonies of all species are smaller than the yearly average in all habitats. In DelMarVa, however, the contrast is much less clear. For barrier beach skimmer colonies, the opposite pattern was found, with new and deserted colonies being much larger than the average.

*Influence of Herring Gulls.*—Colony-site abandonment and establishment are, of course, also influenced by the competitive-predatory effects of Herring Gulls (Crowell and Crowell 1946; Drury 1973, 1974; Nisbet 1971, 1973; Burger 1977, 1979a; Erwin 1980), especially on small bay islands where space is potentially limiting. While Herring Gull presence appears only partly responsible for causing abandonment, it seems to influence site establishment strongly (Table 7). By avoiding gull-occupied sites, the other species are left with fewer alternatives and may be forced into selecting even poorer sites.

## Concluding Remarks

Much additional work remains to be done in the area of sociopsychological aspects of habitat selection. Gulls and terns may be attracted to certain sites by the presence of both conspecifics (Klopfer and Hailman 1965) and heterospecifics (Koskimies 1957). The relative impact of storms, predators, intra- and interspecific competition, etc., varies among years and among colonies (Morris and Hunter 1976, Burger and Lesser 1979), emphasizing the need to conduct long-term studies (Tinkle 1979). The results reported here must be interpreted cautiously, as they are based on only 2 yr of comparable data. Regional colony surveys replicated over a 10–15-yr period using standardized methods would prove to be the most instructive but are nonexistent in North America today.

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## Literature Cited

Bent, A. C. 1921. Life histories of North American gulls and terns. U.S. Natl. Mus. Bull. 112.

Blus, L., & J. Keahey. 1978. Variation in reproductivity with age in the Brown Pelican. Auk 95: 128–134.

Bongiorno, S. 1970. Nest-site selection by Laughing Gulls (*Larus atricilla*). Anim. Behav. 18: 434–444.

Borodulina, T. 1966. Biological and economic import of gulls and terns of southern USSR water bodies. Ecology-morphology of birds and mammals. Jerusalem, Israel Program for Sci. Transl.

Buckley, F. G. 1978. Use of dredged material islands by colonial seabirds and wading birds in New Jersey. U.S. Army Waterways Exper. Sta. Tech. Rept. D-78-1.

———, & P. A. Buckley. 1972. The breeding ecology of Royal Terns, *Sterna* (*Thalasseus*) *maxima maxima*. Ibis 114: 344–359.

Buckley, P. A., & F. G. Buckley. 1977. Human encroachment on barrier beaches of the northeastern U.S. and its impact on coastal birds. Pp. 68–76 *in* A symposium on coastal recreational resources in an urbanizing environment (J. Noyes, Ed.). Amherst, Massachusetts, Massachusetts Coop. Ext. Serv. Monogr.

———, & ———. 1979. What constitutes a waterbird colony? Reflections from the northeastern U.S. Pp. 1–15 *in* Proc. 1979 Conf. Colonial Waterbird Group, Lafayette, Louisiana.

———, & ———. In press. Population and colony site trends of Long Island waterbirds for five years in the mid 1970s. New York, Trans. Linnaean Soc.

Burger, J. 1977. Nesting behavior of Herring Gulls: Invasion into *Spartina* saltmarsh areas of New Jersey. Condor 79: 162–169.

———. 1979a. Nest repair behavior in birds nesting in salt marshes. J. Comp. Physiol. Psychol. 11: 189–199.

———. 1979b. Competition and predation: Herring Gulls versus Laughing Gulls. Condor 81: 269–277.

———, & F. LESSER. 1978. Selection of colony sites and nest sites by Common Terns *Sterna hirundo* in Ocean County, New Jersey. Ibis 120: 433–449.

———, & ———. 1979. Breeding behavior and success in salt marsh Common Tern colonies. Bird-Banding 50: 322–337.

———, & J. SHISLER. 1978. Nest site selection and competitive interaction of Herring and Laughing gulls in New Jersey. Auk 95: 252–266.

COULSON, J. 1968. Differences in the quality of birds nesting in the centre and on the edges of a colony. Nature 217: 478–479.

CROWELL, E., & S. CROWELL. 1946. The displacement of terns by Herring Gulls at the Weepecket Islands. Bird-Banding 17: 1–10.

CUSTER, T., R. OSBORN, & W. STOUT. 1980. Distribution, species abundance, and nest-site use of Atlantic Coast colonies of herons and their allies. Auk 97: 591–600.

DEXHEIMER, M. W., & W. SOUTHERN. 1974. Breeding success relative to nest location and density in Ring-billed Gull colonies. Wilson Bull. 85: 288–290.

DRURY, W. H. 1973. Population changes in New England seabirds. Bird-Banding 44: 267–313.

———. 1974. Population changes in New England seabirds (continued). Bird-Banding 45: 1–15.

———, & I. C. T. NISBET. 1972. The importance of movements in the biology of Herring Gulls in New England. Pp. 173–212 *in* Population ecology of migratory birds: a symposium. U.S. Bureau Sport Fisheries and Wildl., Wildl. Res. Rept. 2.

ERWIN, R. M. 1977. Population and colony site dynamics in selected Massachusetts waterbirds. Pp. 19–25 *in* Proc. 1977 Conf. Colonial Waterbird Group, DeKalb, Illinois.

———. 1979a. Coastal waterbird colonies: Cape Elizabeth, Maine to Virginia. U.S. Fish and Wildl. Serv., Biol. Serv. FWS/OBS 79/10.

———. 1979b. Species interactions in a mixed colony of Common Terns (*Sterna hirundo*) and Black Skimmers (*Rynchops niger*). Anim. Behav. 27: 1054–1062.

———. 1980. Breeding habitat use by colonially nesting waterbirds in two mid-Atlantic U.S. regions under different regimes of human disturbance. Biol. Conserv. 18: 39–51.

———, & C. E. KORSCHGEN. 1979. Coastal waterbird colonies: Maine to Virginia, 1977—an atlas showing colony locations and species composition. U.S. Fish and Wildl. Serv., Biol. Serv., FWS/OBS 79/08.

GALLI, J. 1978. The distribution and status of the colonial waterbirds of New Jersey (Summer 1977) with recommendations for their management. New Jersey Div. Fish, Game, and Shellfisheries, first annual rept.

———. 1979. The colonial waterbirds of New Jersey, Summer 1978. New Jersey Div. Fish, Game, and Shellfisheries, second annual rept.

GOCHFELD, M. 1978. Breeding synchrony in Black Skimmers: colony vs. subcolonies. Pp. 171–177 *in* Proc. 1978 Conf. Colonial Waterbird Group, New York, New York.

GREENHALGH, M. 1974. Population, growth, and breeding success in a salt marsh Common Tern colony. Naturalist 932: 121–127.

HATCH, J. J. 1970. Predators and piracy by gulls at a ternery in Maine. Auk 87: 244–254.

KANE, R., & R. FARRAR. 1976. 1976 coastal colonial bird survey of New Jersey. New Jersey Audubon Occas. Paper No. 125.

———, & ———. 1977. 1977 coastal colonial bird survey of New Jersey. New Jersey Audubon Occas. Paper No. 131.

KLOPFER, P., & J. HAILMAN. 1965. Habitat selection in birds. Adv. in Anim. Behav. 1: 279–303.

KOSKIMIES, J. 1957. Terns and gulls as features of habitat recognition for birds nesting in their colonies. Ornis Fennica 34: 1–6.

MCNICHOLL, M. 1971. The breeding biology and ecology of Forster's Tern (*Sterna forsteri*) in Delta marsh. Unpublished M.Sc. thesis, Winnepeg, Manitoba, Univ. Manitoba.

———. 1975. Larid site tenacity and group adherence in relation to habitat. Auk 92: 98–104.

MONTEVECCHI, W. 1978. Nest site selection and its survival value among Laughing Gulls. Behav. Ecol. Sociobiol. 4: 143–161.

MORRIS, R., & R. HUNTER. 1976. Factors influencing desertion of colony sites by Common Terns (*Sterna hirundo*). Can. Field-Natur. 90: 137–143.

NISBET, I. C. T. 1971. The Laughing Gull in the northeast. Amer. Birds 25: 677–683.

———. 1973. Terns in Massachusetts: present numbers and historical changes. Bird-Banding 44: 27–55.

PARNELL, J., & R. SOOTS, JR. 1980. Atlas of colonial waterbirds of North Carolina. Univ. North Carolina. Sea Grant Publ. UNC-SG-80-06.

PORTNOY, J. 1977. Nesting colonies of seabirds and wading birds—coastal Louisiana, Mississippi, and Alabama. U.S. Fish and Wildl. Serv., Biol. Serv. FWS/OBS 77/07.

RYDER, J. 1975. Egg-laying, egg size, and success in relation to immature-mature plumage of Ring-billed Gulls. Wilson Bull. 87: 534–542.

SOUTHERN, W. 1977. Colony selection and colony site tenacity in Ring-billed Gulls at a stable colony. Auk 94: 469–478.

STONE, W. 1937. Bird studies at Old Cape May. Philadelphia, Delaware Valley Ornithol. Club.

STOREY, A. 1978. Adaptations in Common Terns and Forster's Terns for nesting in the salt marsh. Unpublished Ph.D. dissertation, Newark, New Jersey, Rutgers Univ.

TINKLE, D. 1979. Long-term field studies. BioScience 29: 717.

WILSON, A. 1854. American ornithology. New York, T. L. Magagnos and Co.