Colony Site Selection by Least Terns: Physical Attributes of Sites

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Abstract.—I examined physical characteristics of sites occupied by Least Tern (Sterna antillarum) colonies on Long Island, New York, in comparison to sites without colonies. Contrary to historical records most Least Terns were found on broad sand flats or small rounded areas (knobs) adjacent to inlets, rather than close to the high-tide line on long stretches of beach. This habitat shift is related to overall changes in habitat availability. Humans have usurped most beaches with extensive recreational use, off-road vehicle traffic, and construction. Conversely, man-modified sites suitable for nesting have been created by deposition of dredged soil. In 1976, 98% of Least Tern colonies were on sites that had been graded excellent or good quality in 1975. Although only 48% were on sites more or less free from human disturbance, there was nonetheless a statistically significant preference for sites either remote from human use areas or with little evidence of off-road vehicular traffic. Although social factors and previous experience are of importance in influencing where a Least Tern will nest in a given year, it is possible to predict the Suitability of sites for Least Terns based on estimates of physical Quality (e.g., size, shape, slope, substrate, vegetation), and Availability (freedom from human disturbance). Semiquantitative estimates of Quality and Availability were used to produce a composite Suitability score. Least Terns nested on 67% of the highly suitable, but only 17% of the poorly suited sites. Because of the shortage of suitable undisturbed nesting sites, Least Terns now occupy sites that are suitable in every respect except for a high prevalence of off-road vehicle tracks or other disturbance.

Key Words: Colony selection, Endangered species, Habitat availability, Habitat management, Habitat quality, Habitat suitability, Human disturbance, Least Tern, Sterna antillarum.

Organisms generally occupy only a subset of all the habitats potentially accessible to them. Studies of habitat selection provide insight into basic ethological issues, and in the case of endangered species may be vital for their preservation. My study of colony and nest site selection by Least Terns (Sterna antillarum) involves both physical and social characteristics, and this paper focuses on physical factors influencing colony site selection in this species. Buckley & Buckley (1980a) have discussed both ultimate and proximate factors influencing site selection by seabirds. Important contributions to our understanding of Least Tern habitat selection have been presented by Jernigan et al. (1978) and Thompson & Slack (1982). The latter paper examined many variables for 39 Least Tern colonies on the Texas Coast, and determined the relative contribution of certain variables using a Principal Component Analysis.

Most discussions of habitat selection rely on detailed descriptions of the habitats used by birds. Burger & Lesser (1978) carried such analysis a step further for the Common Tern (S. hirundo) in New Jersey by comparing islands occupied by tern colonies with nearby unoccupied islands. The present study makes a similar comparison for Least Tern colonies on Long Island, New York. I assume that in general colony site selection can be influenced by a) physical attributes of the various available sites, and b) behavioral or social attributes, notably site tenacity and group adherence (Austin 1949, 1951).

The Least Tern, once nearly eliminated from the Atlantic Coast of the United States by hunting for the millinery trade (Bull 1964, Stone 1937), is still a vulnerable species. Both New York and New Jersey have recently placed it on the State Endangered Species lists, and the Pacific Coast race (brownis) is on the Federal Endangered Species list. The recently separated Little Tern, S. albifrons (A.O.U. 1983) has similarly declined in Britain (Cramp et al. 1974). Loss of suitable nesting habitat due to housing or recreational construction and direct disturbance particularly by off-road
vehicles in the nesting colonies, are considered primary factors jeopardizing terns (e.g., Cramp et al. 1974, Massey 1974, Nisbet 1973, Shick 1890). Buckley & Buckley (1980b) sound a more optimistic note for populations in the northeastern United States. In view of the widespread concern over the future of the species, several surveys have been made to estimate the numbers of Least Terns breeding on the Atlantic Coast (e.g., Downing 1973). Elsewhere I have discussed the recent history of the Least Tern population on the western south shore of Long Island (Gochfeld 1973) documenting its recovery there, after extirpation in the late 1800's.

I distinguish habitat selection per se from site tenacity and/or social attraction (Gochfeld 1980). I also use the following terms to characterize sites: Quality, Availability and Suitability. Quality refers to physical and biological attributes of the site. Availability refers to whether the birds can or cannot use the site (because of human disturbance). Suitability is a composite measure referring to all attributes of the site. In this paper I provide some estimates of Quality based on physical features of sites (size and shape, slope, location, substrate, and vegetation), and on availability of the site (freedom from human usurpation or intrusion). Site Suitability can be estimated by an arithmetic composite of Quality and Availability, although in more meaningful terms the Suitability must be determined by the birds themselves in terms of their productivity at a site over a period of years. This paper examines certain measures of Quality and Availability that can be ascertained in the field and applied to estimation of site Suitability without having knowledge of previous site occupancy. Social factors influencing colony site selection will be examined separately.

STUDY AREAS AND METHODS

Study Areas.—On western Long Island, New York I censused most Least Tern colonies between Jones Inlet and Fire Island Inlet from 1972 to 1978. Once a site was used it was checked in subsequent years. Population estimates (±5 pr) were made by approaching the edge of the colony and counting the number of terns getting up from nests. At many colonies most nests were found and marked, but in some cases this was either unfeasible or undesirable.

Aerial Surveys.—Aerial surveys of colonial birds on Long Island were conducted annually from 1975 to 1978 (see Buckley & Buckley 1980b), during which I surveyed virtually all Least Tern colonies as well as unoccupied potential sites. The helicopter surveys covered 2200 air miles over a 3-day period, covering all likely (and many unlikely) areas of beach and landfill, even those in close proximity to cities. It is unlikely that any major concentrations (>100 pairs) of Least Terns were missed. Locations and approximate numbers of nesting Least Terns were recorded in each of these years. No attempt was made to assess productivity.

Both the ground and aerial surveys were made in early-June, hence re-nesting attempts were ignored. For large colonies, the helicopter facilitated counts, because by flying at a height of 10-20 meters parallel to the edge of a colony at 50-80 kmH, we flushed birds sequentially, allowing better estimates than one could make in a colony with the birds swirling around overhead on all sides. In many cases we landed the helicopter near colonies to "ground-truth" the estimates. It was necessary to exercise care to avoid prop-wash disturbance to the eggs. By flying at low elevation we assured that we would flush virtually all Least Terns we passed, although on a few occasions we could see birds remaining on their nests just below us.

In June 1975 I characterized all potential tern nesting sites (see below) with regard to location, dimensions, slope, substrate, vegetation cover, and potential human disturbance. Tern populations were estimated in June, 1976. The 1975 habitat characteristics and 1976 tern population estimates are used in this paper. The use of data from the two different years serves to reduce bias in my habitat descriptions inasmuch as the 1975 descriptions were made prior to the 1976 population estimates.

Definition of Sites.—I defined a site as a geographic location at which a colony of birds may or may not nest. In this paper a colony involves an actual breeding attempt.
LEAST TERN COLONY SITE SELECTION

at a particular site, and a single pair can constitute a colony. A site can be unoccupied in a given year, but by definition a colony cannot be unoccupied.

Although Least Terns formerly nested mainly on undisturbed outer beaches (Bent 1921), their present day nesting sites are more varied. I classified these as beaches (outer beaches or berms), dredged spoil islands, dredged “knobs” (raised rounded or rectangular sites on the barrier beach usually adjacent to inlets), interdune swales, old parking lots, and waste areas with varying kinds of substrates. Roof-nesting is not known to occur in the northeastern United States. In most cases the above areas were clearly circumscribed, but in dealing with long stretches of beach it was necessary to subdivide these in some useful, if arbitrary, way. I delineated stretches of beach by the following kinds of discontinuity: inlets, human facilities (parks, villages, parking lots, roads), salt marshes, points, or promontories. I excluded beaches less than 5 m wide above the high tide line (in effect the line of wrack deposited on the beach), or areas less than 10 x 10 m in size. Salt marshes and lawns were also excluded. Contrary to findings for Little Terns in Great Britain (Norman & Saunders 1969) there were virtually no Least Terns nesting within 5 m of the high tide line.

Variables Studied.—The location of each site was classified as a beach, an island, a knob, or a flat (including for example, interdune areas, spoil deposition sites on the mainland or behind barrier beaches, and old parking lots). I compared occupied and non-occupied sites with respect to the following Quality variables: location, size (length and width in m.), slope (deviation from horizontal in degrees measured with a spirit level), substrate (percent shell or gravel), percent vegetation cover, and the following Availability variables: isolation (proximity in meters to houses or recreation sites) and off-road vehicle (ORV) intrusion (measured by percent of area covered by vehicle tracks). Size estimates were confirmed from aerial photographs. The percent of shell or gravel on the substrate was estimated visually. Substrate was categorized as fine sand (less than 1% shell or gravel), 1-10% shell or gravel, 10-20% shell or gravel, 20-50% shell or gravel, >50% gravel, dry mud, or other. I did not make a more quantitative measure of substrate texture as did Thompson & Slack (1982). Vegetation was mainly Beach Grass (Ammophila breviligulata) or Seaside Goldenrod (Solidago sempervirens). The percent vegetation cover was estimated visually (±10%) and was often confirmed from aerial photographs.

Quality.—I characterized site Quality based on four of the above characteristics (Table 1A): width of site above high tide line, slope, substrate, and vegetation cover.

Availability.—Each site was classified by proximity to human use areas such as houses, uncontrolled roads, or recreational areas (beaches, playgrounds, boat-ramps, picnic grounds). A composite measure of Availability (see Table 1B) was based on proximity to potential human disturbance and on extent of ORV tracks. Actual human intrusion on foot was not measured on the aerial surveys.

Suitability.—A compound measure of habitat Suitability was then determined by multiplying the quality and disturbance scores for each site as shown at the bottom of Table 1C. I arbitrarily classified habitat suitability by the composite score as follows: 1 to 3 as high, 4 to 6 as moderate, and greater than 6 as poor.

RESULTS

Site Characteristics.—Least Tern colonies were on the berm of beaches, on dredged knobs or islands adjacent to inlets and on large flats. Table 2 shows the size and shape of inactive and active sites. It is apparent that despite the availability of many long and thin beaches, supposed to be a favored habitat of the species, terns tended to avoid these and nested instead on wide beaches, knobs, and flats ($\chi^2=6.4, P<0.02, d.f. = 1$).

Table 3 compares the nesting colonies versus the unused sites with respect to their Quality and Availability features. Applying the compound Suitability score the number of occupied and unoccupied sites deemed highly suitable, moderately suitable, and poor were compared in a 2 x 3 contingency table (see Table 4), yielding $\chi^2 = 24 (P<0.001, d.f. = 2)$. Those sites that 1
TABLE 1. Quality, Availability and Suitability criteria for Least Tern colony sites.

A. Quality Criteria

<table>
<thead>
<tr>
<th>Category</th>
<th>Description</th>
<th>Width</th>
<th>Slope degrees</th>
<th>Substrate % shell</th>
<th>Vegetation cover</th>
</tr>
</thead>
<tbody>
<tr>
<td>A</td>
<td>Excellent</td>
<td>&gt;20m</td>
<td>&lt;10</td>
<td>1-10%</td>
<td>&lt;10%</td>
</tr>
<tr>
<td>B</td>
<td>Good</td>
<td>&gt;10m</td>
<td>&lt;20</td>
<td>10-20%</td>
<td>&lt;25%</td>
</tr>
<tr>
<td>C</td>
<td>Fair</td>
<td>&gt;10m</td>
<td>&lt;30</td>
<td>20-50%</td>
<td>&lt;50%</td>
</tr>
<tr>
<td>D</td>
<td>Poor</td>
<td>&lt;10m</td>
<td>&gt;30</td>
<td>0 or &gt;50%</td>
<td>&gt;50%</td>
</tr>
</tbody>
</table>

B. Availability Criteria

<table>
<thead>
<tr>
<th>Position Relative to human use area</th>
<th>Percent Ground Cover by ORV Tracks</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>0%</td>
</tr>
<tr>
<td>Immediate Adjacent</td>
<td>C</td>
</tr>
<tr>
<td>Moderate Distance or with adequate barrier</td>
<td>B</td>
</tr>
<tr>
<td>Remote or Isolated</td>
<td>A</td>
</tr>
</tbody>
</table>

C. Composite Suitability Score

<table>
<thead>
<tr>
<th>Availability</th>
<th>Score</th>
<th>A</th>
<th>B</th>
<th>C</th>
<th>D</th>
</tr>
</thead>
<tbody>
<tr>
<td>A</td>
<td>1</td>
<td>1</td>
<td>2</td>
<td>3</td>
<td>4</td>
</tr>
<tr>
<td>B</td>
<td>2</td>
<td>2</td>
<td>4</td>
<td>6</td>
<td>8</td>
</tr>
<tr>
<td>C</td>
<td>3</td>
<td>5</td>
<td>6</td>
<td>9</td>
<td>12</td>
</tr>
<tr>
<td>D</td>
<td>4</td>
<td>4</td>
<td>8</td>
<td>12</td>
<td>16</td>
</tr>
</tbody>
</table>

*Width of site above high tide line
bOffroad Vehicle

TABLE 2. Relationship between size and configuration of sites and occupancy by nesting Least Terns in 1976.

<table>
<thead>
<tr>
<th>Used for Breeding in 1976</th>
<th>Yes</th>
<th>No</th>
</tr>
</thead>
<tbody>
<tr>
<td>Less than 15 m wide*</td>
<td>1</td>
<td>20</td>
</tr>
<tr>
<td>15-30 m wide (&lt;100 m long)</td>
<td>5</td>
<td>8</td>
</tr>
<tr>
<td>15-30 m wide (150-300 m long)</td>
<td>4</td>
<td>6</td>
</tr>
<tr>
<td>15-30 m wide (&gt;350 m long)</td>
<td>3</td>
<td>16</td>
</tr>
<tr>
<td>30-50 m wide (&lt;150 m long)</td>
<td>9</td>
<td>7</td>
</tr>
<tr>
<td>30-50 m wide (&gt;150 m long)</td>
<td>6</td>
<td>8</td>
</tr>
<tr>
<td>&gt;50 m wide (&lt;200 m long)</td>
<td>6</td>
<td>7</td>
</tr>
<tr>
<td>&gt;50 m wide (&gt;200 m long)</td>
<td>7</td>
<td>9</td>
</tr>
<tr>
<td>Knobs (ca 30x30 to 50x50 m)</td>
<td>4</td>
<td>3</td>
</tr>
<tr>
<td>Summary</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Long &amp; narrow beaches</td>
<td>10</td>
<td>34</td>
</tr>
<tr>
<td>Medium or wide beaches, knobs and flats</td>
<td>35</td>
<td>50</td>
</tr>
</tbody>
</table>

\[ x^2 = 6.4, P < 0.02 \]

*Regardless of length

judged as highly suitable in 1975, showed a much greater tendency to be occupied in 1976, than did sites that I had judged to be moderately or poorly suitable.

Certain site attributes (particularly vegetation cover and ORV tracks) can change between years. To determine whether the 1975 habitat judgements were a suitable surrogate for the potentially biased 1976 data, I found a high between-year correlation for estimates of vegetation cover (Median value 12% in 1975 and 15% in 1976; Kendall \( \tau = 0.88, P < 0.001 \)) and track cover (Median Value 20% in 1975 and 25% in 1976; Kendall \( \tau = 0.71, P < 0.001 \)). For only 9% of sites was there a change in Suitability category between years. One site with heavy (90%) track cover in 1975 had no track cover in 1976. Otherwise no change exceeded 25%.

The percent vegetation cover and off-road vehicle track cover were grouped. For each of these groupings the geometric mean colony size was computed. Figure 1A
TABLE 3. Occupancy of sites in relation to Quality, Availability, and Suitability, shown in 2 x 2 contingency tables.

<table>
<thead>
<tr>
<th>Occupancy</th>
<th>Quality</th>
<th>Availability</th>
<th>Suitability</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>High</td>
<td>Low</td>
<td></td>
</tr>
<tr>
<td>Occupied</td>
<td>45</td>
<td>1</td>
<td>22</td>
</tr>
<tr>
<td>Not Occupied</td>
<td>48</td>
<td>40</td>
<td>24</td>
</tr>
</tbody>
</table>

% Occupied Sites in "High" category:
- High Quality: 98%
- Availability: 48%
- Suitability: 48%

Chi Square:
- Quality: 26.6
- Availability: 5.6
- Suitability: 18.6

P < 0.001 < 0.025 < 0.001

High Quality and Availability correspond to A & B grades shown in Table 1; Low Quality and Availability correspond to C & D grades. High Suitability is a composite score of 1-3 (see Table 1C).

TABLE 4. Comparison of Habitat Suitability for Sites used and not used by Long Island Least Terns in 1976.

<table>
<thead>
<tr>
<th>Suitability</th>
<th>Colony Sites</th>
<th>Unused Sites</th>
</tr>
</thead>
<tbody>
<tr>
<td>High</td>
<td>24</td>
<td>12</td>
</tr>
<tr>
<td>Medium</td>
<td>13</td>
<td>32</td>
</tr>
<tr>
<td>Poor</td>
<td>8</td>
<td>40</td>
</tr>
</tbody>
</table>

\[ \chi^2 = 23.4 \ df = 2 \ P < 0.01 \]

shows the percent of sites occupied by nesting terns as a function of the percent of vegetative cover. A peak occurs at 5-10%, with about 60% of such sites used for nesting. However, the pattern of colony size as a function of vegetation (Fig. 1B) is less impressive. As most of the colonies were on sites with 5-25% vegetation, it is notable that with 10% cover the mean colony size was 14 pairs, greater than colony size with either 5% or 25% cover. The anomalous value of 20 pairs for the occupied sites with 30% vegetation cover is unexplained.

During the aerial surveys the number of sites with extensive vehicle track cover was high. However, most of the tern colonies were on sites with less than 20% track cover. Figure 2A shows no clear pattern except that with more than 45% track cover, sites were unlikely to be occupied. The anomalous point for 80% track cover (with 2 of 4 sites occupied) is unexplained. Figure 2B shows that the mean colony size is larger on sites with less than 20% track cover, except for one very large colony with 65% track cover. Although the relationship between nesting and vehicle tracks (Fig. 2B) is in-
consistent, it remains apparent that sites with less track cover were more likely to be occupied.

The Gilgo Beach Colony.—From 1968 to 1976 up to 60 pairs of Least Terns nested at various points on the 2 km stretch of beach east of the now razed Gilgo Coast Guard Station (Gochfeld 1976). The width of the Gilgo Beach is relatively consistent within any breeding season, but varies dramatically from year to year. From 1971 to 1976 reproductive success was consistently poor (<0.1 young/pair) and in three of six seasons no young were fledged. During these years the berm was narrow (<20m) and nests were subject to both flooding and human disturbance. In the fall of 1976 the Army Corps of Engineers initiated a beach nourishment project in which mud and sand dredged from Fire Island Inlet (about 7 km to the east) was pumped as a slurry through a pipe, and deposited on the beach to widen and stabilize it. By spring of 1977 the beach was more than 100 m wide from the base of the outer dune to the high tide line. In that year more than 350 pairs of Least Terns nested there, and despite heavy pressure from off-road vehicles, picnickers, frequent incursions of dogs and tourists, the colony fledged at least 80 young (0.27 young/pair). The following year, although the berm had not narrowed significantly, the breeding population dropped to about 100 pairs, and by 1982 when the beach had eroded to about 20-30 m, the tern population was down to about 40 pairs.

DISCUSSION

Historical Information.—I reviewed the past century’s literature on Least Terns to find evidence of changes in habitat utilization or geographic differences in habitats used. The relative abundance of this species in the mid-19th century is described by Bent (1921). The vulnerability of Least Terns and their habitats has long been recognized. Shick (1890) reported that New Jersey Least Terns were “forsaking their former breeding grounds on account of the new seaside resorts…”

In Virginia in the 1870’s colonies were scattered along most of the barrier beach areas. The population was presumably large for over 1000 were killed in a day and about 100,000 in a season (Bent 1921); this toll eventually reduced the Atlantic coast population to but a small remnant. Nisbet (1973) provides a detailed discussion of the recent status of this species in the northeastern United States.

Nesting Habitat.—Least Terns have been considered to prefer open habitats with scant vegetation (Bent 1921, Thompson & Slack 1982; see also Schonert 1961 for Little Tern). Because of vegetational succession and/or erosion, this preferred habitat may be characterized as ephemeral, and the species is said to adopt a “fugitive” strategy (e.g., Buckley & Buckley 1980b), moving readily from one site to another, rather than showing high site tenacity. Erwin (1978) and Burger (in press) discuss the relatively high turnover rates of Least Terns, and Burger (in press) notes that the reputed high turnover rates for this species is exaggerated.

Bent (1921) characterized Least Tern habitats as broad, flat, open sandy beaches devoid of vegetation, with a substrate comprising stones and shells. He recognized that unlike most other terns, the Least Terns nested on mainland or barrier beaches in preference to islands. Stone (1937) considered the Least Tern characteristic of extensive undisturbed beaches where they nested just above the high tide mark. On Cape Cod Least Tern colonies were distributed along the least accessible beaches (Austin 1929). Burroughs (1966) concluded that the species required the close proximity of water, a pebble substrate for egg camouflage, as well as sparse vegetation to provide shade for chicks.

Least Terns do not nest on salt marsh, and in the northeastern United States they seem to shun coarse gravel substrates, though such habitats are certainly used elsewhere. In various parts of its range it nests on barren beaches (Downing 1973, Massey 1974), riverine sandbars (Ganier 1930, Hardy 1957); dirt fill or dredged spoil (Massey 1974, Jernigan et al. 1978), and gravel roof-tops (Fisk 1975). In the Caribbean the Least Tern nests on small sandbars projecting from islets and cays (Pelzl 1969), on islands in salt ponds (Fletcher 1980), and on little used airport aprons (personal observation).
Along the Texas Coast, Thompson & Slack (1982) found 29% of colonies on barrier islands, 35% on the mainland, and 38% on "other islands," mainly on dredged spoil. The inland race, S. a. athalassos, nests mainly on riverine sandbars (Ganier 1930, Hardy 1957), a habitat preferred also by the Yellow-billed Tern, S. superciliaris, a South American member of the same superspecies. However, the coastal antillarum does not occupy riverine sandbars even a short distance inland (Tomkins 1959). In California, Least Terns nest on beaches adjacent to estuaries, with a sand-shell substrate, relatively devoid of vegetation as well as on artificially managed sites (Massey 1974, Swickard 1974).

British Little Terns nest mainly on shingle and shell beaches with little or no vegetation (Cramp et al. 1974), and in 70% of cases colonies were less than 2 m. above high tide line (Norman & Saunders 1969). In Germany, sandy or gravel beaches along the sea are preferred, although the species formerly bred on inland lakes and rivers (Schonert 1961).

**Long Island Tern Colonies.**—The preferred sites for Least Tern colonies on Long Island appear to be on the berm at the base of the outer dune or on sandy flats or fill areas. On broad sandy beaches Least Terns spread themselves widely over the beach, and on sandbars or spits they may occupy the entire crown of the sandy portion. The Gilgo beach-nourishment project, conversely had a beneficial (if short-lived) effect by substantially widening the eroded beach at Gilgo. Concomittantly, the Gilgo Least Tern colony grew from 50 to 350 pairs, following nourishment, then declined to 40 pairs as the beach narrowed.

**Elevation.**—Elevation above high tide is clearly an important criterion of breeding success in Least Terns. Prior to beach nourishment, the Gilgo Least Tern colony was flooded out in the early summer storms of 1972. Thompson & Slack (1982) found that measures of colony elevation were of primary importance as a characteristic of Texas Least Tern colonies, with a loading exceeding +0.9 on the first Principal Component Axis, which itself explained 38.5% of the variance among colonies. Norman & Saunders (1967) reported that 64 of 87 Little Tern colonies were less than 2 m above high tide, and that storm tides were important causes of colony destruction.

**Substrate.**—Least Terns may nest on a variety of substrates, preferring coarse sand mixed with shell. On Long Island very fine sand subject to wind drifting is shunned. Terns often nest on the slightly elevated patches of coarse sand and shell that build up on sandy beaches. Terns will also nest on firm earth fill or loose gravel, where there is no sand. Few Long Island sites offer coarse shell substrate such as the oyster-shell bars of the southeastern United States. Rocky beaches are not used for nesting on Long Island. Thompson & Slack (1982) reported that sand and shell fragment content had the highest loading (>0.9) on the second Principal Component Axis which explained 18% of variance among colonies. They had four natural sites with more than 95% shell and fragments, but nearly 33% of the colonies clustered at 80-90% sand with less than 20% shell, a finding comparable to the Long Island data. They report an apparent preference for fine material, while warning that dredged spoil silt may have an adverse effect because eggs may become glued to the substrate. Neither their study nor this one did a comparative study of substrates among used and unused sites, so the relationship between substrate texture and colony site preference remains to be examined. In Britain most Little Tern colonies are on shingle beach; few occupy strictly sandy sites (Norman & Saunders 1967).

**Vegetation.**—Although most Least Tern colonies are nearly devoid of vegetation, traditional sites may continue to be occupied as vegetational succession progresses so long as open habitat remains. In 76% of 46 colonies vegetative cover was less than 20%, although adjacent areas were often heavily vegetated. In 52% of these colonies cover was less than 10%. Thompson & Slack (1982) report that cover rarely exceeded 20% at the 39 colonies they examined. Vegetation cover had a loading > +0.8 on their 3rd Principal Component, which explained 16% of the colony variance. Norman & Saunders (1967) report that most British Little Tern colonies contained no vegetation at all.
Disturbance.—Burger (1981) summarized the ways in which human disturbance adversely affects colonial water birds. Least Terns are considered particularly vulnerable to disturbance (Buckley & Buckley 1976) because their preferred habitats, the ocean front beaches, suffer heavy human recreational use, while off-road vehicles driving through their colonies kill young or cause them to scatter. On Long Island significantly more lightly (A or B) than heavily (C or D) disturbed sites were occupied by Least Terns (Table 3). Although only 48% of the occupied sites were categorized A or B with respect to disturbance, this reflects the high prevalence of disturbance occurring on the kinds of sites favored by the species. Moreover, because disturbance adversely affects productivity (Burger in press, Gochfeld, unpublished data), and future occupancy of a site is influenced by productivity (Burger in press), disturbed sites are less likely to become major colony sites.

In view of the threat that off-road vehicles on beaches pose to nesting Least Terns, I was dismayed by the prevalence of vehicle tracks on almost every mainland beach, neck or bar, and even on islands where trail bikes had apparently been transported by boats. Even in the state park areas in which Least Terns were found nesting, vehicular tracks were evident near colonies.

CONCLUSIONS

Estimates of habitat Quality and Availability, allow one to make at least semi-quantitative judgement of the Suitability of a particular site for successful breeding of Least Terns. Among the sites examined one could predict Least Tern usage based on size, shape and slope of site, general substrate, vegetative cover, and extent of or potential for human disturbance. The importance of previous colony occupancy will be examined in another paper.

Of the sites occupied in 1976 (see Table 3) 98% had been categorized A or B with respect to habitat quality and 48% were categorized A or B with respect to disturbance (compared with 34% of all sites). Beaches narrower than 10 m. above high tide were avoided by terns, even though the overall area available might be large (due to their length). Sites with greater than 20% vegetative coverage were not often occupied, and most occupied sites had less than 33% of their surface covered by vehicle tracks. However, sites that had been used previously, were not necessarily abandoned when these limits were exceeded.

Although physical attributes of a site are of obvious importance in avian habitat selection the importance of social factors should not be underestimated. In a study of the Black Skimmer Rynchops niger, (Gochfeld 1978) I concluded that site tenacity and social interactions were more prominent determinants of colony or sub-colony location, than were physical or botanical features of the site. Despite the high turnover rates reported for the Least Tern, site tenacity may be a more important determinant of site selection, than are subtle variations in the physical characteristics.

Site tenacity can be determined by a) successful reproduction at the site, b) stability of the site, c) large colony size, and d) lack of specific adverse factors. I conclude that initial colony site selection by experienced birds is based on a) physical qualities and appearance of the terrain, b) relatively low disturbance, c) proximity to a former breeding site, and d) occupancy by other Least Terns. Naive birds breeding for the first time should either return to their natal colony (their own fledging and survival pointing to the suitability of that site) or should join other birds at another site, an act that may not require independent judgement of habitat quality or habitat selection in the typical sense of the word.

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LITERATURE CITED


