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MODELING COLONY-SITE DYNAMICS: A CASE STUDY OF GULL-BILLED TERNS (*STERNA NILOTICA*) IN COASTAL VIRGINIA

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ABSTRACT.—We developed a Markov process model for colony-site dynamics of Gull-billed Terns (*Sterna nilotica*). From 1993 through 1996, we monitored breeding numbers of Gull-billed Terns and their frequent colony associates, Common Terns (*Sterna hirundo*) and Black Skimmers (*Rynchops niger*), at colony sites along 80 km of the barrier island region of coastal Virginia. We also monitored flooding events and renesting. We developed the model for colony survival, extinction, and recolonization at potential colony sites over the four-year period. We then used data on annual site occupation by Gull-billed Terns to estimate model parameters and tested for differences between nesting substrates (barrier island vs. shellpile). Results revealed a dynamic system but provided no evidence that the dynamics were Markovian, i.e. the probability that a site was occupied in one year was not influenced by whether it had been occupied in the previous year. Nor did colony-level reproductive success the previous season seem to affect the probability of site occupancy. Site survival and recolonization rates were similar, and the estimated overall annual probability of a site being occupied was 0.59. Of the 25 sites that were used during the four-year period, 16 were used in one or two years only, and only three were used in all four years. Flooding and renesting were frequent in both habitat types in all years. The frequent flooding of nests on shellpiles argues for more effective management; augmentation with shell and sand to increase elevations as little as 20 cm could have reduced flooding at a number of sites. The low colony-site fidelity that we observed suggests that an effective management approach would be to provide a large number of sand and/or shellpile sites for use by nesting terns. Sites not used in one year may still be used in subsequent years. *Received 2 September 1997, accepted 19 March 1998.*

POPULATIONS OF GULL-BILLED TERNS (*Sterna nilotica*) have declined in coastal Virginia and elsewhere along the Atlantic Coast, with numbers in Virginia dropping from about 2,000 breeding individuals in the mid-1970s to between 600 and 800 from 1990 to 1995 (Williams et al. 1990, and unpublished reports). Low productivity has been suspected over the past decade, and few immature birds have been seen in late summer (B. Truitt pers. obs.). Gull-billed Terns (hereafter "gull-bills") nest on two types of habitats along the Atlantic Coast: (1) sandy beaches on barrier islands, and (2) small (<0.5 ha) storm-deposited shellpiles along the fringes of saltmarsh islands in coastal lagoons. Gull-bills are subjected to different selection pressures in these two habitat types. Storm events (averaging >22 per year in coastal Virginia; Davis and Dolan 1993) are much more dramatic in changing the profile of barrier islands than shellpiles. Also, predators (including Herring Gulls [*Larus argentatus*], raccoons [*Procyon lotor*], and red foxes [*Vulpes fulva*]) are more abundant on barrier islands than on shellpiles (B. Truitt pers. obs., N. Moncrief pers. comm.). On the other hand, barrier islands often attract large numbers of other sand-nesting species that may be rare or absent on shellpiles. Species such as Common Terns (*Sterna hirundo*) and Black Skimmers (*Rynchops niger*), as well as conspecifics (Ray et al. 1991, Boulinier and Danchin 1997, Danchin and Wagner 1997), may serve as important cues to favorable nesting sites for gull-bills (Erwin 1979, Parnell and Soots 1979, Forbes and Kaiser 1994, Brown and Rannala 1995). Common Terns and Black Skim-

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mers arrive at colony sites in early to mid-May, at about the same time as gull-bills, although the two former species often lay eggs later than do gull-bills (Erwin 1977).

In addition to relying on current physical and biological cues in selecting colony sites, previous experience at a site may influence the choice of nesting location in some species (see Greenwood and Harvey 1982, Anderson et al. 1992). The breeding success of individual females at a nesting site (Lokemoen et al. 1990, Nager et al. 1996), the success of nearby colony neighbors, or even the success of birds at other colony sites (assessed via prospecting birds; see Boulinier et al. 1996, Boulinier and Danchin 1997, Danchin and Wagner 1997), may affect colony-site choice the next year. Thus, at least for some species, it is conceivable that individuals gain cues for predicting reproductive performance at several spatial scales: their own nest, the neighborhood level, their entire nesting colony, and even the metapopulation of colony sites in making subsequent colony choices. The selection process becomes an exercise in optimal stochastic control, and habitat assessment may include both current and past conditions and the covariance between these conditions and reproductive success (Williams and Nichols 1984, Nichols 1996).

Here, we model the presence and absence of Gull-billed Tern colonies at particular sites as a function of local extinction and colonization probabilities. These models provide for rigorous hypothesis testing that is not possible when colony-site extinctions, colonizations, and annual differences are combined into one "colony-site turnover index" as in previous studies (e.g. Erwin et al. 1981). We used these models to address general questions about the year-specificity of extinction and colonization probabilities and about the extinction-colonization process. We speculated that probabilities of local extinction and/or colonization might be influenced by habitat (shellpile vs. barrier island) and by the relative size of the colony. Specifically, we predicted that: (1) physical and/or predator disturbances on barrier islands would result in higher turnover (higher probabilities of extinction and colonization) between years than on shellpile habitats in marshes; (2) larger numbers of conspecifics (social attraction) at a site would result in lower site turnover (i.e. higher site tenacity); and (3) one of the site-dynamic parameters, local extinction, would be influenced by colony-level reproductive success. In addition to these tests involving site-dynamic parameters, we tested the hypothesis that shellpile and barrier island sites did not differ in average colony size (i.e. number of birds) during years of occupancy.

METHODS

Surveying.—From 1993 to 1996, we attempted to locate all Gull-billed Tern colonies along the Atlantic coast of Virginia using aircraft and boats as part of a cooperative effort involving The Nature Conservancy, USGS Patuxent Wildlife Research Center, and the University of Virginia's Long-term Ecological Research (LTER) project. One to three observers visited each site from late May to July, 2 to >10 times per year, and made accurate counts of adult gull-bills and other associated species. For small colonies (<50 pairs), we counted all nests and multiplied by two for the adult count. For larger colonies, one to three observers made counts of all species and recorded the average number of adults per species. Where multiple counts were made in a given year, we used the highest number for analyses. After flooding events each year, we revisited sites from one to three weeks later to document renesting attempts. We used the number of adults to compare colony sizes. Therefore, when nest counts were made, we multiplied by two to arrive at an "adult count." We considered a site to be "occupied" by a colony if it contained at least five nests. All colony sites were revisited in all years following their initial location. In addition, knowledge of the areas searched each year permitted some colony sites to be designated as "not occupied" in years prior to their initial identification as a colony site.

To evaluate the influence of previous nesting success on site reoccupancy, we used the results from a companion study on nesting success conducted from 1994 to 1996 (R. M. Erwin unpubl. data) and categorized each colony site as successful (i.e. if any nesting pairs produced fledglings) or unsuccessful (no fledglings produced). Owing to logistical constraints, we determined nesting success at only 22 colony sites in 1994 and 1995. We then conducted a separate analysis to determine whether success status in year i was associated with occupancy in year $i + 1$. We did not need to use the full model for this test, because the test focused on local extinction probability and not on colonization probability.

Habitats.—We were not able to obtain quantitative data on habitat change at colony sites because this would have required sophisticated laser theodolite surveying. Although this methodology is available at this LTER site, reliable survey benchmarks were not in place to accurately survey all of the sites (R. Carlson pers. comm.). Visual assessments revealed that all colony sites were overwashed by seawater at least once each fall/winter, and that the barrier island sites, at least qualitatively, were more highly modified between years than were the shellpiles. Dunes and overwash fans often were entirely restructured between years. Despite small changes in their shapes, shellpiles were consistent in location and size from year to year.

We attempted to keep records of flooding events. Records were more complete in 1995 and 1996 than in 1993 or 1994. We scored each colony site into one of three categories: no flooding losses of eggs or young, partial flooding losses, or complete flooding losses. Small sample sizes required that we combine categories to conduct statistical tests.

To assess the influence of habitat on colony size, we compared colony sizes by species between the two habitats using nonparametric Wilcoxon two-sample tests. We considered only colonies with five or more nesting pairs. For comparisons, we calculated mean colony sizes for Gull-bills, Common Terns, and Black Skimmers over all years and colony sites.

Modeling colony dynamics.–Our approach to testing hypotheses about colony dynamics was to develop a general probabilistic model for the data and then to constrain model parameters and use likelihood-ratio tests to assess the adequacy of the constrained models. This approach is similar in some respects to that used in modeling capture-recapture data (e.g. Lebreton et al. 1992) and species presence/absence data at single locations (Rosenzweig and Clark 1994).

The data consisted of the presence or absence of bird colonies at specific locations. We conditioned the analysis on colony sites that were occupied during at least one year of the study. All colony sites were visited each year following their initial identification as a colony site in order to determine status (i.e. whether breeding birds were present). Sites were only included in the analysis for years in which their status was known. Colony sites were identified by general habitat type (barrier island or shellpile) and by colony size (large sites had more than the median number of birds per colony; small sites had fewer than the median number of birds).

We define the following model notation: $n_i^{k,g}$ = number of colony sites in state k (0 = no breeding birds present, 1 = breeding birds present) in site group g (1 = large colony, barrier island; 2 = large colony, shellpile; 3 = small colony, barrier island; 4 = small colony, shellpile), in year i; $m_i^{k,g}$ = number of $n_{i-1}^{k,g}$ colony sites that contain breeding birds in year i; ϕ_i^g = probability that a site in group g with breeding birds in year i also has breeding birds in year $i + 1$ ($1 - \phi_i$ can be viewed as a local extinction probability); and γ_i^g = probability that a site in group g with no breeding birds in year i has breeding birds in year $i + 1$ (γ_i can be viewed as a local immigration or colonization probability).

The probability that exactly $m_i^{1,g}$ of the $n_{i-1}^{1,g}$ colony sites occupied in year $i - 1$ will again be occupied in year i, conditional on the number of occupied sites ($n_{i-1}^{1,g}$) in year $i - 1$, is given by:

$$\Pr(m_i^{1,g})|n_{i-1}^{1,g}, \phi_{i-1}^g) = \frac{(n_{i-1}^{1,g})!}{(m_i^{1,g})!(n_{i-1}^{1,g} - m_i^{1,g})!} \times (\phi_{i-1}^g)^{m_i^{1,g}} \times (1 - \phi_{i-1}^g)^{[n_{i-1}^{1,g} - m_i^{1,g}]}. \quad (1)$$

The probability that exactly $m_i^{0,g}$ of the $n_{i-1}^{0,g}$ colony sites not occupied in year $i - 1$ will again be occupied in year i, conditional on the number of unoccupied sites in year $i - 1$, is given by:

$$\Pr(m_i^{0,g})|n_{i-1}^{0,g}, \gamma_{i-1}^g) = \frac{(n_{i-1}^{0,g})!}{(m_i^{0,g})!(n_{i-1}^{0,g} - m_i^{0,g})!} \times (\gamma_{i-1}^g)^{m_i^{0,g}} \times (1 - \gamma_{i-1})^{[n_{i-1}^{0,g} - m_i^{0,g}]}. \quad (2)$$

The probability model for the entire data set ($m_i^{k,g}$; $i = 2, 3, 4$; $k = 0, 1$; $g = 1, 2, 3, 4$) is given by the product of these conditional probabilities over all of the values of indices i, k, and g.

A different (yet equivalent) way of writing the probability would involve conditioning on colony sites used at some time during the study and then treating the number of sites following the different possible patterns of colony-site dynamics as conditional multinomial random variables. For example, assume that a colony site identified in period 1 showed the following site history, where 0 denotes absence and 1 donates presence: 1 1 0 1 . This history reflects a site that had birds only in periods 1, 2, and 4. The probability associated with this history, conditional on an active colony site in group g at period 1, would be written as: $\phi_1^g(1 - \phi_2^g)\gamma_3^g$. These equivalent models are somewhat analogous to capture-recapture modeling based on sufficient statistics (e.g. Jolly 1965) versus capture histories (e.g. Seber 1965).

Model-fitting, estimation, and testing were carried out using program SURVIV (White 1983) with models coded by J. E. Hines. Likelihood-ratio tests were used to test for specific sources of variation, and AIC values (Akaike 1973, Burnham and Anderson 1992) were used to determine which models were the most useful for parameter estimation.

The most general model (ϕ_i^g, γ_i^g) contained time-specific parameters that differed by site group. This model allows full interaction between the group characteristics habitat type and colony size. Reduced-parameter models constrained survival and colonization probabilities to be constant over group and/or time in order to test hypotheses about time and group effects ([ϕ_i, γ_i], [ϕ^g, γ^g], [ϕ, γ]). We also fit linear-logistic models that permitted main effects associated with both group characteristics with no interaction. In addition, we modeled survival and col-

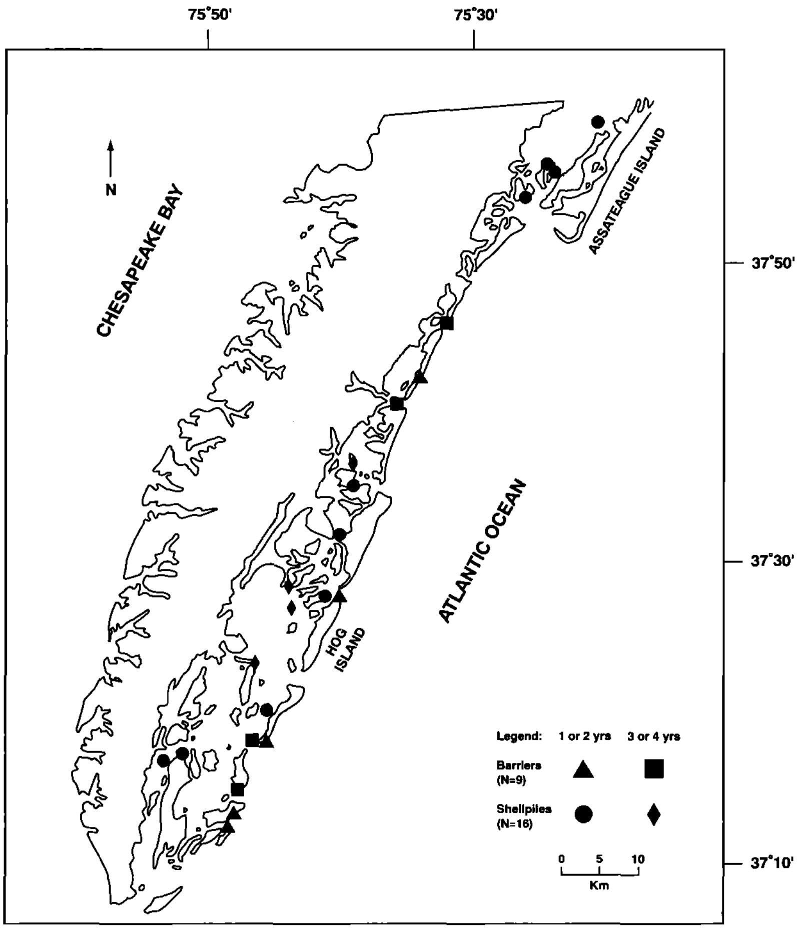

FIG. 1. Colony-site use by Gull-billed Terns from 1993 to 1996, showing sites used on shellpile and barrier island habitats during one to two versus three to four years along the eastern shore of Virginia.

onization as dependent on single group characteristics. Specifically, in models ($\phi_i^{g(s)}$, $\gamma_i^{g(s)}$) and ($\phi_i^{g(h)}$, $\gamma_i^{g(h)}$), survival and colonization depended only on colony size and habitat, respectively. All of these models, and their survival and colonization parameters, assume that colony-site dynamics reflect a first-order Markov process in which colony state (occupied or unoccupied) at time i depends on state at time $i - 1$. Another possibility is that site dynamics are not Markovian. For example, the non-Markovian model ($\phi_i^g = \gamma_i^g$) specifies that the probability that a site is occupied at time $i + 1$ is given by a single parameter, regardless of the previous history of the site (i.e. regardless of the occupancy state at time i).

RESULTS

The use of colony sites was highly dynamic in the four years of study. Of the 25 sites used during the study, only three were used in all four years. Most colony sites (16 of 25) were used only once or twice during the four years (Fig. 1).

Models of colony-site dynamics.—Point estimates of survival and colonization probabilities varied substantially over time (Table 1), and we found evidence of time-specificity in these parameters ([ϕ_i^g, γ_i^g] vs. [ϕ^g, γ^g], $\chi^2 = 29.8$, df = 14, $P < 0.01$; [ϕ_i, γ_i] vs. [ϕ, γ], $\chi^2 = 10.2$, df = 4, $P = 0.03$; [$\phi_i = \gamma_i$] vs. [$\phi = \gamma$], $\chi^2 = 4.4$, df = 2, $P = 0.11$). There was no strong evidence that site group characteristics were important determinants of survival or colonization probabilities, either when considered together with interactions ([ϕ_i^g, γ_i^g] vs. [ϕ_i, γ_i], $\chi^2 = 24.6$, df = 16, $P = 0.08$), or separately for colony size ([$\phi_i^{g(s)}$, $\gamma_i^{g(s)}$] vs. [ϕ_i, γ_i], $\chi^2 = 7.9$, df = 6, $P = 0.24$)

TABLE 1. Parameter estimates (estimated SE in parentheses) for colony survival and colonization probabilities in Gull-billed Terns under different models of colony dynamics.

Parameter	Model				
	$[\phi_i^g, \gamma_i^g]$	$[\phi^g, \gamma^g]$	$[\phi_i^{g(s)}, \gamma_i^{g(s)}]$	$[\phi_i^{g(h)}, \gamma_i^{g(h)}]$	$[\phi_i, \gamma_i]$
			Large barrier island		
ϕ_{93}^{1}	0.80 (0.179)	0.77 (0.117)	0.50 (0.177)	0.67 (0.192)	0.43 (0.132)
ϕ_{94}^{1}	0.75 (0.217)	0.77 (0.117)	0.67 (0.192)	0.75 (0.217)	0.50 (0.158)
ϕ_{95}^{1}	0.75 (0.217)	0.77 (0.117)	0.80 (0.126)	0.57 (0.187)	0.76 (0.103)
γ_{94}^{1}	>0.99 (<0.001)	0.50 (0.354)	>0.99 (0.447)	0.80 (0.179)	0.79 (0.110)
γ_{95}^{1}	<0.01 (<0.001)	0.50 (0.354)	<0.01 (<0.001)	0.50 (0.354)	0.38 (0.171)
			Large shellpile		
ϕ_{93}^{2}	<0.01 (0.577)	0.55 (0.150)	0.50 (0.177)	0.25 (0.153)	0.43 (0.132)
ϕ_{94}^{2}	0.50 (0.354)	0.55 (0.150)	0.67 (0.192)	0.33 (0.192)	0.50 (0.158)
ϕ_{95}^{2}	0.83 (0.152)	0.55 (0.150)	0.80 (0.126)	0.90 (0.095)	0.76 (0.103)
γ_{93}^{2}	0.50 (0.354)	0.71 (0.171)	0.50 (0.354)	0.54 (0.204)	0.33 (0.157)
γ_{94}^{2}	>0.99 (0.500)	0.71 (0.171)	>0.99 (0.447)	0.78 (0.139)	0.79 (0.110)
γ_{95}^{2}	<0.01 (<0.001)	0.71 (0.171)	<0.01 (<0.001)	0.33 (0.192)	0.38 (0.171)
			Small barrier island		
ϕ_{93}^{3}	<0.01 (<0.001)	0.25 (0.217)	0.33 (0.192)	0.67 (0.192)	0.43 (0.132)
ϕ_{95}^{3}	0.33 (0.272)	0.25 (0.217)	0.71 (0.171)	0.57 (0.187)	0.76 (0.103)
γ_{93}^{3}	<0.01 (0.577)	0.50 (0.177)	0.29 (0.171)	<0.01 (<0.001)	0.33 (0.157)
γ_{94}^{3}	0.75 (0.127)	0.50 (0.177)	0.67 (0.157)	0.80 (0.179)	0.79 (0.110)
γ_{95}^{3}	>0.99 (<0.001)	0.50 (0.177)	0.50 (0.204)	0.50 (0.353)	0.38 (0.171)
			Small shellpile		
ϕ_{93}^{4}	0.40 (0.219)	0.54 (0.138)	0.33 (0.192)	0.25 (0.153)	0.43 (0.132)
ϕ_{94}^{4}	0.25 (0.500)	0.54 (0.138)	0.25 (0.217)	0.33 (0.192)	0.50 (0.158)
ϕ_{95}^{4}	>0.99 (0.500)	0.54 (0.138)	0.71 (0.171)	0.90 (0.095)	0.76 (0.103)
γ_{93}^{4}	0.50 (0.250)	0.50 (0.134)	0.29 (0.171)	0.50 (0.204)	0.33 (0.157)
γ_{94}^{4}	0.60 (0.219)	0.50 (0.134)	0.67 (0.157)	0.78 (0.139)	0.79 (0.110)
γ_{95}^{4}	0.40 (0.219)	0.50 (0.134)	0.50 (0.204)	0.33 (0.192)	0.38 (0.171)

or habitat ($[\phi_i^{g(h)}, \gamma_i^{g(h)}]$ vs. $[\phi_i, \gamma_i]$, $\chi^2 = 10.0$, df = 6, $P = 0.12$). Point estimates of survival and colonization rates did not differ in a consistent manner (Table 1), and we found no evidence to support the Markov process model ($[\phi_i, \gamma_i]$ vs.$[\phi_i = \gamma_i]$, $\chi^2 = 5.9$, df = 3, $P = 0.12$). Thus, the probability that a colony site was occupied at any time i did not appear to depend on whether that colony site was occupied at time $i - 1$. However, when considering this conclusion, it is important to recall that our modeling was restricted to sites at which a colony was present for at least one of the four years of study.

TABLE 2. Akaike's Information Criterion (AIC), number of parameters, and goodness-of-fit statistics for various models of colony-site dynamics in Gull-billed Terns.

Model	AIC	Parameters	χ^2	df	P
$[\phi_i^g, \gamma_i^g]$	67.2	22	—	—	—
$[\phi_i^{g(s)}, \gamma_i^{g(s)}]$	63.9	12	13.1	12	0.36
$[\phi_i^{g(h)}, \gamma_i^{g(h)}]$	61.8	12	11.3	12	0.50
$[\phi_i^g = \gamma_i^g]$	63.9	12	13.1	12	0.36
$[\phi_i, \gamma_i]$	59.9	6	19.9	18	0.34
$[\phi^g, \gamma^g]$	69.0	8	23.2	16	0.11
$[\phi_i = \gamma_i]$	59.8	3	24.6	21	0.27
$[\phi, \gamma]$	62.1	2	27.5	22	0.19
$[\phi = \gamma]$	60.2	1	27.5	23	0.23

The three-parameter model ($\phi_i = \gamma_i$) with a separate probability for colony occupancy each year had the lowest AIC of all tested models (Table 2), fit the data reasonably well ($\chi^2 = 24.6$, df = 21, $P = 0.27$), and was judged the most appropriate for this data set. Under this model, the estimated annual probabilities of site occupancy were: $\hat{\phi}_{93} = \hat{\gamma}_{93} = 0.39$ ($\widehat{SE} = 0.102$), $\hat{\phi}_{94} = \hat{\gamma}_{94} = 0.67$ ($\widehat{SE} = 0.096$), and $\hat{\phi}_{95} = \hat{\gamma}_{95} = 0.64$ ($\widehat{SE} = 0.096$). Recall that these parameters (ϕ_i, γ_i) correspond to the probability that the site is occupied in year $i + 1$. The single-parameter model ($\phi = \gamma$) also had a low AIC and fit these data reasonably well (Table 2), so there was no strong evidence of year-specific variation. The estimate of colony site occupancy under model ($\phi = \gamma$) was 0.57 ($\widehat{SE} = 0.058$).

TABLE 3. Colony sizes of Gull-billed Terns and associated species at mixed-species colonies in coastal Virginia, 1993 through 1996. Values under habitat are mean number of adults, with number of colonies in parentheses.

Species	Habitat		
	Barrier island	Shellpile	P-value[a]
Gull-billed Tern	66 (24)	31 (33)	>0.10
Common Tern[b]	382 (15)	36 (23)	<0.01
Black Skimmer[b]	340 (17)	40 (10)	0.11

[a] Wilcoxon two-sample test.

[b] Includes 1993 data from Watts (1994).

TABLE 4. Frequency of flooding in Gull-billed Tern colonies in coastal Virginia, 1994 through 1996 combined. Values are number of colonies.

Habitat	Flooding losses in colony		
	None	Partial	Complete
Barrier island	4	4	0
Shellpile	4	6	6

All of the models considered thus far have permitted estimation of parameters associated with colony-site occupation in three different years, 1994, 1995, and 1996. The restriction to these years resulted from our *a priori* expectation that colony-site dynamics would follow a first-order Markov process. However, the finding that the Markovian assumption was not necessary permits us to estimate the probability of site occupancy in 1993, as well as to estimate the probability of occupancy for other years using slightly more data (it was not necessary that occupancy status be known in years i and $i + 1$ in order to estimate the probability of occupancy in year $i + 1$). We used the full data set to estimate annual probabilities of site occupancy as: 0.61 ($\widehat{SE} = 0.102$) for 1993, 0.42 ($\widehat{SE} = 0.101$) for 1994, 0.68 ($\widehat{SE} = 0.093$) for 1995, and 0.64 ($\widehat{SE} = 0.096$) for 1996. Although the point estimate was lower for 1994 than for the other three years, this difference was not significant using the full data set ($\chi^2 = 4.1$, df = 3, $P = 0.25$). The annual probability of site occupancy for all four years was estimated to be 0.59 ($\widehat{SE} = 0.050$).

Nesting success and local extinction.–Nesting success in year i seemed to have little effect on the probability of colony site occupancy in year $i + 1$ (Fisher's exact test, $P = 1.0$). Six of nine colony sites where total nesting failure occurred in one year were occupied by birds the next year. For sites where at least partial nesting success occurred, 8 of 13 had returning birds the next year.

Influence of habitat on colony size.–The proportion of gull-bills nesting on the shellpile habitat varied from a low of 0.20 in 1993 to 0.47 in 1995. Although the mean colony size (number of adults) on barrier islands was double that on shellpiles, the difference was not significant (Wilcoxon two-sample test, $Z = 0.62$, $P > 0.1$; Table 3), although colony-size variation and limited samples resulted in a test with low power. Differences were clearer when we compared colony sizes of associated species in the two habitats. Numbers of Common Terns ($Z = 3.38$, $P < 0.01$) and Black Skimmers ($Z = 1.61$, $P = 0.11$) in mixed-species colonies on barrier islands were an order of magnitude larger than those on the small shellpile habitats with gull-bills (Table 3). Again, with Black Skimmers, small samples and large variation in numbers limited the power of the test. In only two colonies did we find gull-bills nesting in colonies devoid of skimmers and other species of terns (i.e. in conspecific colonies).

Habitat and flooding frequency.–Related to colony-site shifts, flooding appeared to be more frequent on shellpiles than on the barrier islands that we examined (Table 4); however, the habitat comparison for 1993 to 1996 yielded no significant difference (Fisher's exact test, $P = 0.36$; data from partial and complete flooding cells combined). Birds tended to renest in the same year at the same sites, even after a washover. For example, at 16 sites with partial or complete flooding during 1994 to 1996, renesting occurred in the same year at 13 sites.

DISCUSSION

The use of general probabilistic models of colony-site dynamics appears to be a reasonable approach to investigating such systems. Unlike the use of a single colony-site turnover index (see Erwin et al. 1981), these models allow separate estimates of extinction and colonization probabilities and permit testing effects of year, habitat, and/or colony size.

Colony-site use from year to year may be viewed as a stochastic process and does not seem to depend on habitat type for Gull-billed Terns nesting in coastal Virginia. Occupancy of a site in a given year does not seem to depend on whether the site was used in the previous year (i.e. the process is non-Markovian), or on whether birds were at least partially successful in producing young at the site in the previous season (Nager et al. 1996, Boulinier and Danchin 1997). Moreover, whatever cues terns are using to make colony-site choices, the attributes associated with site attractiveness appear to show little spatial consistency from year to year.

Gull-bills, like other marsh-nesting species such as Forster's Terns (*Sterna forsteri*) and Common Terns, face many uncertainties in site selection, primarily predation and flooding (Storey et al. 1988). The presence of predators may be obvious at the time of colony-site selection in some cases (e.g. nesting gulls) but not in others (e.g. mammalian predators). With flooding, few effective cues exist as to the magnitude or frequency of such events during the nesting season. High-water events often are associated with a northeastern exposure for mid-Atlantic coastal marshes during the nesting season (Davis and Dolan 1993). Forster's Terns may avoid such locations in some marshes (Storey 1987a, b); however, during summer, high-water events often are associated with winds from the southeast or southwest. Forster's Terns may be able to select among a broad range of colony sites, whereas gull-bills must select among sites with some minimum area and/or elevation of shells along marsh margins with more exposure than areas used by Forster's Terns. Furthermore, because gull-bills historically have nested both on beaches and in marshes (Parnell et al. 1995), they may not "fine-tune" their responses in the way that obligate marsh-nesting species do (Storey et al. 1988).

Our evidence provided little support for a social-attraction hypothesis. Conspecific colony size did not seem to be important in the model. The very limited support that we found was that two of the three sites used in all four years had large numbers of gull-bills, Common Terns, and Black Skimmers. However, the largest colony that we monitored (Cedar Sandbar) for three years had very low nesting success and thus was unlikely to function as a source of recruits (R. M. Erwin unpubl. data)

We were unable to identify factors associated with abandonment of colonies between years. All shellpiles were present in all four years, although minor changes in topography occurred in some places. At one shellpile, the expansion of a colony of Herring Gulls and Great Black-backed Gulls (*Larus marinus*) in 1995 and 1996 into an area that had been occupied by gull-bills in 1994 may have caused abandonment. As mentioned above, topographic changes on the barrier islands seemed to be more significant than on shellpiles. More significantly, mammalian predators may have been responsible for the abandonment of another barrier island colony in 1995 and 1996. Apparently, red foxes had recolonized the island, because many tracks and several dens were found (B. Truitt pers. obs.). In addition to abandonment by terns, no gulls nested on the island in 1995 or 1996.

Previous nesting success often is a good indicator of habitat quality (Burger 1982, Klopfer and Ganzhorn 1985, Burger and Gochfeld 1990, Danchin and Monnat 1991, Nager et al. 1996), and knowledge of previous nesting success and/or success of neighbors (or even of birds at other sites) may influence the choice of future colony sites (Boulinier et al. 1996, Boulinier and Danchin 1997). Results from a related study (R. M. Erwin unpubl. data) suggest that gull-bills had very poor fledging success in all three years (1994 through 1996) in both habitats. Thus, the lack of consistent differences in success between the two habitats may help explain why we found no differences in estimates of colony-site survival and colonization between habitats.

MANAGEMENT AND CONSERVATION

In 1995 and 1996, the high frequency of flooding resulted mostly from abnormally high spring tides, not from storm events. Most of the nest losses at shellpiles resulted from flooding in the three years of our study (R. M. Erwin unpubl. data). Because gull-bills and other species nest on a number of these small piles, sometimes for several consecutive years, elevating these habitats by as little as 20 cm with shell and sand would be an inexpensive, effective way to improve nesting success. Because shellpiles often are only 0.1 to 0.2 ha in size, volume requirements for shell material would be minimal. The current practice of dredging and relocating oyster shell in coastal Virginia exclusively for shellfish restoration means that allocations of shell for nesting terns would require coordination with several other resource management agencies. Alternatively, dredged material from channel maintenance could be used to augment existing shellpiles, as long as the material was a sand-shell mixture. In addition to shellpile management, barrier islands could be enhanced with bulldozers and the addition of sandy dredged materials. Because of frequent overwash events, however, managing barrier islands would require more frequent treatment than would shellpiles.

Because nearly half of the Gull-billed Terns nesting in Virginia use shellpile habitats in some years, and because of low site fidelity (as low as 0.39 in 1994), we suggest that managers protect and/or enhance shellpile habitat on a number of sites in the coastal region to allow terns many choices in habitat selection. This will become especially critical as barrier island habitats are increasingly occupied by gulls and mammalian predators.

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