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Nest-site selection and hatching success of waterbirds in coastal Virginia: some results of habitat manipulation

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ABSTRACT. Rising sea levels in the mid-Atlantic region pose a long-term threat to marshes and their avian inhabitants. The Gull-billed Tern (Sterna nilotica), Common Tern (S. hirundo), Black Skimmer (Rynchops niger), and American Oystercatcher (Haematopus palliatus), species of concern in Virginia, nest on low shelly perimeters of salt marsh islands on the Eastern Shore of Virginia. Marsh shellpiles are free of mammalian predators, but subject to frequent floods that reduce reproductive success. In an attempt to examine nest-site selection, enhance habitat, and improve hatching success, small (2 × 2 m) plots on five island shellpiles were experimentally elevated, and nest-site selection and hatching success were monitored from 1 May to 1 August, 2002. In addition, location, elevation, and nesting performance of all other nests in the colonies were also monitored. No species selected the elevated experimental plots preferentially over adjacent control plots at any of the sites. When all nests were considered, Common Tern nests were located significantly lower than were random point elevations at two sites, as they tended to concentrate on low-lying wrack. At two other sites, however, Common Tern nests were significantly higher than were random points. Gull-billed Terns and American Oystercatchers showed a weak preference for higher elevations on bare shell at most sites. Hatching success was not improved on elevated plots, despite the protection they provided from flooding. Because of a 7 June flood, when 47% of all nests flooded, hatching success for all species was low. Nest elevation had the strongest impact on a nest's probability of hatching, followed by nest-initiation date. Predation rates were high at small colonies, and Ruddy Turnstones (Arenaria interpres) depredated 90% of early Gull-billed Tern nests at one shellpile. The importance of nest elevation and flooding on hatching success demonstrates the potential for management of certain waterbird nesting sites. Facing threats from predators on barrier islands and rising sea levels especially in the mid-Atlantic region, several species of nesting waterbirds may benefit dramatically with modest manipulation of even small habitat patches on isolated marsh islands.

SINOPSIS. Selección del lugar de anidamiento y éxito de eclosionamiento de aves acuáticas en costa de Virginia: algunos resultados de la manipulación del habitat

El incremento en los niveles del mar en la region del Atlántico medio presenta un peligro a largo alcance a los marjales y las aves que los habitan. Especies como *Sterna nilotica, S. hirundo, Rynchops niger* y *Haematopus palliatus,* son especies de particular preocupación porque anidan en el perímetro bajo de Islas en marjales salinos en la costa este de Virginia. Los marjales con acumulaciones de guijarros están libres de depredadores, pero sujetos a inundaciones frecuentes que reducen el éxito reproductivo. En un intento de examinar la selección de nido, mejorar el habitat y el éxito de eclosionamiento, pequeños lotes de 2 × 2 metros fueron elevados (experimentalmente) en cinco islotes con guijarros, y se monitoreo la selección de lugares para anidar y el éxito de anidamiento del 1 de mayo al 1 de agosto de 2002. Además se monitoreo la localización, elevación y el desempeño de anidamiento de todas las otras especies en las colonias. Ninguna especie seleccionó de forma preferencial, los lotes elevados experimentalmente, sobre los predios adjacentes utilizados como control. Cuando examinamos todos

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los nidos estudiandos, encontramos que los nidos de *S. hirundo* estaban localizados significativamente más bajos que los puntos con elevación al azar en dos de los lugares, y tendieron a concentrarse en los lugares menos elevados. En otras dos localidades los nidos de *S. hirundo* se encontraron significativamente más altos que los puntos al azar. *S. nilotica* y el ostrero mostraron una débil preferencia por lugares más elevados con guijarros en la mayoria de las localidades estudiadas. El éxito de eclosionamiento no mejoró sustancialmente en los lotes elevados, no empece a la protección que estos ofrecieron a eventos de inundabilidad. Debido a una inundación que ocurrió el 7 de junio, en donde el 47% de los nidos se inundaron, el éxito de eclosionamiento para todas las especies resultó bajo. La elevación de los nidos tuvo su mayor impacto en la probabilidad de eclosionar, seguido por la fecha de iniciación de la anidada. La tasa de depredación resultó alta en colonias pequeñas.

Key words: American Oystercatcher, Black Skimmer, coastal Virginia, Common Tern, Gull-billed Tern, habitat manipulation, Haematopus palliatus, Rynchops niger, sea-level rise, shellpiles, Sterna hirundo, S. nilotica

Gull-billed Terns (Sterna nilotica), Common Terns (S. hirundo), Black Skimmers (Rynchops niger), and American Oystercatchers (Haematopus palliatus) nest on storm-deposited shellpiles on the perimeters of salt marsh islands and on barrier island beaches in the barrier islandlagoon complex that characterizes the Eastern Shore of Virginia (Fig. 1). Most shellpiles have low elevations, and may be subject to flooding from spring high tides and storm surges during the breeding season, leading to frequent nesting failures (Burger and Lesser 1979; Erwin et al. 1998; Eyler et al. 1999). Total inundation of shellpile habitats and marshes occurs more often than on barrier islands (B. R. Truitt, pers. comm.; Burger and Gochfeld 1991; Eyler et al. 1999). Because of the dual threats of mammalian predators on barrier islands and frequent flooding, safe nesting sites for waterbirds are limited in coastal Virginia (Erwin et al. 2001, 2003). The reduction in the quantity of suitable breeding habitat may continue if the predicted rise of > 40 cm in sea level in this century increases flooding of coastal lagoons (National Academy of Sciences 1987). For Virginia, Erwin et al. (in press) found that lagoonal marsh elevations are not keeping up with the pace of local relative sea-level rise.

Numbers of colonial Gull-billed Terns, Common Terns, and Black Skimmers nesting on Virginia's barrier islands have declined by 95%, 84%, and 86%, respectively, from 1975 to 1999 (Williams et al. 1990; B. Williams, pers. comm.), and American Oystercatcher numbers have declined by more than 50% on Virginia barrier islands over the last 20 yr (Davis et al. 2001). Because of habitat loss, growing numbers of mammalian predators, rising sea levels, and declining waterbird numbers, management of waterbird breeding sites may become increasingly necessary in an attempt to ameliorate losses. Habitat enhancement by ma-

nipulation of nesting sites needs to be attempted as a method to reduce the frequency of flooding, and to determine methods to create and/or protect existing nesting sites that will be suitable during times of higher sea levels.

Nest-site selection in waterbirds is influenced by a number of physical factors including elevation, substrate, slope, exposure to wind and waves, and cover (see Buckley and Buckley 1980). Because of the high flooding risk on shellpiles, the elevation of a nest is expected to have a strong influence on nest success as higher nests are less likely to be destroyed by flooding. Gull-billed Terns and American Oystercatchers seem to prefer higher nest sites in some regions (Clapp et al. 1983; Lauro and Burger 1989), and American Oystercatchers used elevated platforms for nesting in Virginia (Nol and Humphrey 1994). In an experiment using artificially constructed wrack-mats in New Jersey,

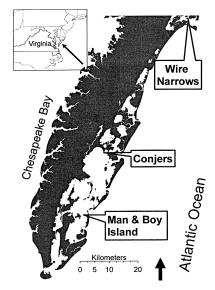


Fig. 1. Map of the Eastern Shore of Virginia, showing locations of study sites.

both Common Terns and Black Skimmers preferred higher elevation mats (Burger and Gochfeld 1990). Because flooding is a major cause of nest failure among waterbirds nesting on shellpiles in Virginia (Eyler et al. 1999), and higher nest sites provide greater protection against flooding and nest failure, species are expected to select higher nest sites than are randomly available on the shellpile.

In addition to physical factors, social factors are also important in nest-site selection. Competition for nest space in colonial-nesting species can be very intense (Buckley and Buckley 1980), especially when nesting areas are limited, such as on shellpiles. Competition for territories is both inter- and intraspecific, with birds arriving first at the site having an advantage in nest-site selection.

Ground-nesting birds are vulnerable to predation, and therefore nest spacing and presence of concealing vegetation are important factors influencing nest-site selection and reproductive success (Buckley and Buckley 1980). For example, Ruddy Turnstones (*Arenaria interpres*) are well-known egg predators that have depredated tern and skimmer colonies worldwide (Crossin and Huber 1970; Parkes et al. 1971; Loftin and Sutton 1979; Farraway et al. 1986; Burger and Gochfeld 1990).

Habitat enhancement by manipulation of nesting sites needs to be attempted as a method to reduce the frequency of flooding, and to determine methods to develop and/or protect nesting sites that will be suitable during times of higher sea levels. The overall objectives of this study were to determine: (1) how four species of waterbirds differ in their nest-site choices, (2) how biological and physical factors affect that choice, (3) whether manipulation of habitat elevation influences nest-site choice, and (4) whether manipulation of habitat elevation could improve hatching success on marsh shellpiles. We expected that elevation would be an important variable for all four nesting species because of the threats of flooding observed previously.

METHODS

Study area. A barrier island-lagoon complex extends about 100 km from Chincoteague Bay to Kiptopeke Point along the eastern shore of the Delmarva Peninsula, Virginia (Fig. 1).

Some salt marsh islands within the lagoons have storm-deposited oyster shellpiles along their perimeters. The shellpiles have higher elevations than the surrounding marsh, and vegetation (primarily smooth cord grass [Spartina alterniflora]) is present on lower-lying areas of some shellpiles. Wrack (dead vegetation mats of either Spartina spp. or eelgrass [Zostera marina]) deposited by high tides and storms often ring the shellpiles, sometimes covering the ridges. Five shellpiles were chosen for this study based on their use by nesting waterbirds in 2001 (R. Rounds, pers. obs.) and previous years (Erwin et al. 1998). The two Wire Narrows shellpiles are located in Chincoteague Bay at 75°23'W, 37°56′N, the two Conjers shellpiles in Hog Island Bay at 75°44'W, 37°28'N, and Man and Boy Island at 75°50′W, 36°17′N.

Experimental elevation of plots. From 11-14 March 2002, before the focal species arrived at the shellpiles to nest, plots on the shellpiles were experimentally elevated. Six sets of paired plots (one elevated, one control) were created at four of the shellpiles, with four paired plots created at the smaller South Conjers shellpile. The location of the paired plots was randomly determined by laying a meter tape down along the length of the long axis of the shellpile, and using a random number table to determine the distance to the first plot of each pair. The status of this plot (elevated or control) was also determined randomly. Each elevated plot was contoured to be similar to its paired control plot. For example, if a control plot was located across a ridge, the elevated plot was contoured to include a ridge. Wrack was also added to elevated plots where necessary. Experimental plots were built 15-20 cm higher than control plots and were roughly 2 × 2 m in area. Based on previous findings at the shellpiles, we believed this area was sufficient for at least four pairs of terns or skimmers to establish nests. Control and elevated plots were at least 1 m apart, and there was at least 1 m between each pair of plots. All experimental plots were elevated using oyster shell from lower or outlying areas of the shellpile not used by nesting birds.

Random points. Twenty-five random points were located on the entire area of each shellpile in early spring before the birds arrived to nest. Random points were located by using measuring tapes and a random number table to determine the distance and direction to a ran-

dom point from a fixed location. The substrate (shell, wrack, or a combination of the two) of each random point was recorded. The exposure of a point to open water was also recorded as exposed, protected, or neutral. Exposed sites were slopes facing open bay waters, protected sites faced marsh, and neutral sites were on the middle ridges of the shellpiles.

Nest monitoring. Shellpiles were monitored twice a week for nesting activity from 1 May to 1 August 2002. Time at the colonies was minimized (usually less than 30 min), and visits during mid-day heat were avoided. After clutches were initiated, nests were marked with 25 cm nails hammered into the shellpile within 6-8 cm of the nest, and a metal tag with nest number and species was tied to the nail. All nests on the shellpiles were monitored. The following was recorded during each visit: species, content of the nest, substrate, exposure, and whether the nest was within 30 cm of vegetation. If a nest scrape was empty, we tried to determine whether the nest had hatched or failed. Empty nests were examined for evidence of flooding or predation. All nests with eggs that disappeared before hatching without any evidence of nest fate (e.g., flooding) were assumed depredated. Eggs were also routinely felt for temperature and signs of abandonment. We assigned new nest numbers for renesting attempts in a previously used scrape. We monitored nests only until hatching, because determining fledging success is logistically difficult without using enclosures (Eyler et al. 1999).

The date of nest initiation (first egg laid) was recorded for each nest. If the exact date was not known, an approximate date was determined from the date of later-laid eggs or by back-calculating from the hatch date. On 7 June a large flood destroyed 47% of all nests. Nests initiated before the flood are considered "early" nests, while those initiated after 7 June are considered "late" nests.

Elevation and GPS. The elevation of random points was measured using a laser level, and the elevation and location of nests was measured using a laser total station. Elevation for all points was recorded as meters above mean sea level, where mean sea level is defined as the arithmetic mean of hourly tide heights (NOAA 2000). Tidal amplitude in Virginia's eastern shore bays is generally about 1.0 m (NOAA 2002). Some nest stakes (<10%) were

lost during the course of the season, and these nests were omitted from elevation and nearestneighbor comparisons.

Statistical analysis. To determine if birds nested in experimentally elevated plots at different frequencies than in control plots, Fisher's exact test was used based on an expected 50–50% distribution of nests between experimental and control plots.

All further statistical tests included data from all nests on the shellpiles. The elevation of nests on the shellpiles was compared to randompoint elevations to determine if birds selected nest sites at significantly different elevations than what was generally available. Before the breeding season, we conducted power analyses using UnifyPow (O'Brien 1998) and SAS (SAS 2001) to determine the sample size of nests and random points needed to detect differences in elevation. Our goal was to sample enough points to have a 90% or greater chance of detecting a 10 cm or greater difference in elevation. The power analysis was used to determine if 25 random points were enough for t-test comparisons between random-point elevation and nest elevation. We compared random-point elevations to a series of hypothetical elevation data for nests. After the season, t-tests were used to test for differences between means for random points versus nest elevations.

To determine if there were temporal changes in nest elevations, we compared early and late nest elevations using t-tests. To determine selectivity of certain substrates (shell, wrack or shell-wrack), we used chi-square analyses of contingency tables to compare the frequency of nests versus random points on each substrate. Similar contingency tables were constructed to compare nest distribution on exposed, protected, and neutral sites compared to random points.

All nests that had at least one egg hatch were considered successful nests. To determine whether hatching success differed between experimental and control plots, we used chisquare tests to compare the frequency of hatching on each plot type. All further analyses included all nests on the shellpiles. To examine the influence of elevation on hatching success, logistic regressions were used with "hatched" or "not hatched" as the dependent variable. We conducted the analyses for three groups: all nests, early nests, and late nests.

Table 1.	Number of nests of for	ır waterbird species iı	1 experimentally el	levated and contr	ol plots in coastal
Virginia.	There were no difference	es in the frequencies	of nests in experi	mental versus co	ntrol plots at any
site based	l on Fisher's exact test ^a . S	Sample size was not la	arge enough for an	alysis at North (Conjers.

	Total number of	Number of nests (percentage of total nests at each site)		
Site	nests on shellpile	Experimental plots	Control plots	
Wire Narrows West	315	19 (6)	10 (3)	
Wire Narrows East	177	4 (2)	5 (3)	
Man and Boy	189	5 (3)	5 (3)	
South Conjers	100	8 (8)	15 (15)	
North Conjers	30	2 (7)	0 (0)	

^a Chi-square analysis df = 1. Wire Narrows West χ^2 = 2.8, P = 0.1; Wire Narrow East χ^2 = 0.11, P = 0.7; Man and Boy χ^2 = 0.0, P = 0.1; South Conjers χ^2 = 2.1, P = 0.14.

The area of each shellpile, and that of the nesting habitat used, that was flooded on 7 June was measured using the GPS coordinates of flooded nests and analyzed with ArcView 3.2 (ESRI 2002). To determine if temporal differences existed in flooding rates, the frequency of flooding at each shellpile of early versus late nests was analyzed using chi-square analysis. We used tests to test for differences between means for elevations of flooded nests and non-flooded failed nests, and also between non-flooded failed nests and successful nests

We assessed the influence of substrate on hatching success using a chi-square test, comparing hatching frequency between shell, wrack, and shell-wrack substrates. Seasonal differences in predation rates were compared using chi-square analysis. The effect of nearest-neighbor distance on hatching success was analyzed using a logistic regression where "hatched" or "not hatched" was the dependent variable. We used multiple logistic regression to determine which factors (nest elevation, nearest-neighbor distance, clutch size, and nest-initiation date) were most important in predicting hatching success, with "hatched" or "not hatched" as the dependent variable

We used SAS (SAS 2001) for all analyses, except nearest-neighbor distances that were calculated from the GPS data using the Distances function in SPSS (SPSS 2001). We calculated nearest neighbor distances for the distance from a nest to its nearest neighbor regardless of species.

RESULTS

Nest-site selection. Utilization of control and elevated experimental plots for nesting was

similar (Table 1). At only two of the five shellpiles was the observed number of nests on elevated experimental plots greater than the number on control plots, and at no shellpile was there a statistically significant difference between the number of nests on each type of plot.

Using a standard deviation of 12.2 cm (based on 25 random points measured prior to nesting), the power analysis showed that with a sample size of 25 random points and 50 nests, our statistical tests would meet our discrimination goal. In fact, we obtained elevation measurements at > 50 nests, thus yielding power > 90% for our statistical tests for detecting differences in elevation.

At the entire colony level, Common Tern nests at both Wire Narrows shellpiles (55% of all Common Tern nests on the shellpiles) were significantly lower (P < 0.05) than the random points, while at the Conjers shellpiles, Common Tern nests were significantly higher than random points (20% of all nests, Fig. 2). At three shellpiles, late Common Tern nests were significantly higher than early nests (Wire Narrows West, $t_{185} = -2.93$, P < 0.01, N = 187nests; Wire Narrows East, $t_{142} = -10.34$, P <0.001, N = 139 nests; Man and Boy, $t_{142} =$ -3.74, P < 0.001, N = 153 nests). Gull-billed Tern nests were significantly higher (P < 0.01) than random points at only one of three colonies (Fig. 2). Black Skimmer nests were not different in elevation from random points (P >0.6). American Oystercatcher nests tended to be higher (but not significantly so, P > 0.05) than random points (Fig. 2).

At all sites, nest substrates and exposures were chosen significantly differently (P < 0.05

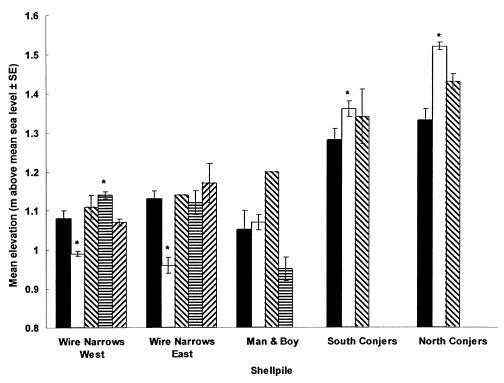


Fig. 2. Nest elevation compared to random-point elevation at five shellpiles for Common Terns, Gull-billed Terns, Black Skimmers, and American Oystercatchers. Asterisk indicates a significant difference between nest elevations and random-point elevations. Wire Narrows West, Common Tern, $t_{212} = -4.75$, P < 0.01, Gull-billed Tern, $t_{34} = 2.86$, P < 0.01; Wire Narrows East, Common Tern. $t_{162} = -4.76$, P < 0.001; South Conjers, Common Tern, $t_{115} = 2.51$, P < 0.05; North Conjers, Common Tern, $t_{34} = 6.53$, P < 0.001. All other results P > 0.1. and a random point; \Box Common Tern; \Box American Oystercatcher; \Box Gull-billed Tern; \Box Black Skimmer.

for all species) from that randomly available. Overall, Common Terns utilized wrack on exposed slopes (39% of all nests at five sites), while Gull-billed Terns (three sites), Black Skimmers (two sites), and American Oystercatchers (five sites) utilized shell on neutral slopes (62%, 61%, and 58% of all nests, respectively).

Distance to the nest of a nearest neighbor for terns and skimmers was low, usually < 2 m, whereas the more solitary American Oystercatcher nests were usually > 20 m apart. Many early tern nests were located near oystercatcher nests, and these nest locations seemed to become centers for the future colony and were used throughout the breeding season.

At the Wire Narrows colonies, nesting Laughing Gulls (*Larus atricilla*) on marsh adjacent to the shellpiles did not appear to affect

nest-site selection by terns on the shellpile colonies (R. Rounds, pers. comm.). Neither of the larger gulls in the region nested within the shellpile habitat on any of the sites, so nest-site competition with gulls was not a factor.

Hatching success. There was no difference in hatching success between nests on control and experimentally elevated plots for Common Terns and Gull-billed Terns (χ^2_1 , P > 0.05, Table 2). Data were insufficient for testing for Black Skimmers and American Oystercatchers. At South Conjers, the only shellpile where any experimentally elevated plots flooded, five nests were lost from control plots and one from an elevated plot. At three other shellpiles, control plots flooded while their paired elevated plot did not; however, no nests were located on these control and elevated plots.

However, when examining all nests on the

	Number of nests (percentage hatched)			
Species	Experimental plots	Control plots		
Common Tern	15 (60)	26 (42)		
Gull-billed Tern	13 (62)	9 (89)		
Black Skimmer	7 (57)	0		
American Oystercatcher	2 (0)	1 (100)		

Table 2. Number of nests and hatching success of four waterbird species in experimentally elevated plots in coastal Virginia.

shellpiles, elevation had a significant positive effect on hatching success for Common Terns at four shellpiles (Table 3). When early and late nests were analyzed separately, however, hatching success was improved with increased elevation only in early nests at three of the shellpiles (Table 3). Hatching success actually improved for lower-elevation nests in late-season Gullbilled Terns at Wire Narrows West (Table 3). Hatching success of Black Skimmers was not affected by nest elevation.

A major flood episode began on 7 June, continuing for a week. During this time period, 47% of all the nests on all shellpiles were flooded. On 7 June, the actual tide in Wachapreague Channel (NOAA 2002) was 0.45 m higher than the predicted tide (Virginia Institute of Marine Science 2002). Although most nests were flooded on 7 June, a few more were lost later in the week. On 14 June, the highest high tide reading was 1.9 m above mean lowest low water (0.4 m higher than predicted), was the highest reached in summer 2002 (NOAA 2002), and was the highest reading since 1979 for that date (NOAA 2002). This flood had major effects on all five sites. Wire Narrows West had the largest amount of used habitat flooded (42%), while Man and Boy had the smallest area of used habitat flooded (22%). The number of nests in the area of the shellpile flooded on 7 June decreased from early to late nests (for example, at Wire Narrows East 85% of early nests were in flooded area versus 11% of late nests) at all shellpiles except Wire Narrows West (which remained the same). Some nests were also lost to flooding during the late May spring high tides and in late July, but these tides did not reach the extent of early June.

For all shellpiles except North Conjers, significantly more (P < 0.001) early nests flooded than late nests because of the high-water period of 7 June (Wire Narrows West, 37% vs. 2%,

 $\chi^2_1 = 52.2$, N = 309; Wire Narrows East, 73% vs. 1%, $\chi^2_1 = 89.8$, N = 177; Man and Boy, 52% vs. 0%, $\chi^2_1 = 53.0$, N = 178; South Conjers, 69% vs. 30%, $\chi^2_1 = 15.0$, N = 99). For all the shellpiles (excluding North Conjers) there was a significant difference (P < 0.001) between the elevations of flooded nests and nests that failed for other reasons. The elevation of failed nests that did not flood was not significantly different from the elevation of nests that hatched. This indicates that the failure of low elevation nests is due to flooding and not other factors that cause nest failure.

At Wire Narrows East and Man and Boy, Common Terns had higher hatching success on shell-wrack and shell than did nests on wrack (Wire Narrows East $\chi^2_2 = 15.7$, P < 0.001, N = 140; Man and Boy, $\chi^2_2 = 8.5$, P < 0.05, N = 152; all other sites, P > 0.1). Wrack is generally found on lower areas of the shellpile where it is deposited by tides, and wrack nests were lower than shell nests at four sites (Rounds 2003). All sites yielded higher hatching success for Common Terns and Gull-billed Terns on sites protected from tides and waves.

Nearest-neighbor distance had a significant negative correlation (logistic regression, Wire Narrows West, $\chi^2_1 = 9.0$, P < 0.01; Wire Narrows East, $\chi^2_1 = 6.7$, P < 0.01) with hatching success for Common Terns at two shellpiles; nests closer together had higher hatching success. At two other sites, the results were not significant (P > 0.1). At Wire Narrows West, the only colony site with sufficient samples of Black Skimmer and Gull-billed Tern nests, we found no significant differences in hatching success as a function of nearest-neighbor distance (P > 0.1 for both tests).

At all five shellpiles there were no statistically significant differences in the frequency of predation between early- and late-season nests (Table 4). However, variation in predation rates

Table 3. Relationship between elevation (reported as mean \pm 1 SE, N in parentheses) and hatching success in three waterbird species in coastal Virginia. The effect of elevation on hatching success was analyzed with a logistic regression, with hatched or not-hatched as the dependent variable, for all nests, early nests, and late nests.

		All nests			Early nests	
Site	Species	Hatched	Failed	χ^2	Hatched	
Wire Narrows West						
	Common Tern Gull-billed Tern Black Skimmer	1.02 ± .007 (83) 1.13 ± .01 (39) 1.07 ± .01 (26)	- (/	19.1*** 4.7* 0.3	1.04 ±.01 (27) 1.13 ± .02 (14) 1.07 ± .02 (22)	
Wire Narrows East Man and Boy	Common Tern	1.08 ± .01 (57)	0.9 ± .02 (52)	27.1**	1.14 ± .04 (7)	
,	Common Tern	$1.14 \pm .02 (72)$	$0.97 \pm .03 (69)$	15.8***	$1.19 \pm .03 (25)$	
South Conjers North Conjers	Common Tern	$1.14 \pm .02 (34)$	$1.32 \pm .02 (54)$	7.2***	$1.43 \pm .09 (5)$	
Tvortii Conjeis	Common Tern	$1.52 \pm .02 (9)$	1.5 ± .01 (12)	0.6†		

 $^{^{}a} df = 1, P > 0.1, *P < 0.05, **P < 0.01, ***P < 0.001.$

among shellpiles was found in the early season primarily because 62% of early-season nests at North Conjers were depredated (Table 4). Ruddy Turnstones had a substantial impact on nest success in Gull-billed Terns (Fig. 3) primarily in very early-season nests, but were not seen on the shellpiles after 21 June. On 19 May, a Ruddy Turnstone was observed depredating nests on Wire Narrows East. A visit to the colony found that nine Gull-billed Tern nests had been depredated. In total, Ruddy Turnstones depredated twelve of the first 14 Gull-billed Tern nests on Wire Narrows East.

Gull-billed Terns and Black Skimmers were the only species that had more nests hatch (Fig. 3) than fail. American Oystercatchers had the lowest nest success, with a conservative estimate of 26% of nests succeeding to hatch, although the fate of 32% of nests was unknown. A multiple logistic regression was used to determine the variables (elevation, date of nest-initiation, clutch size or nearest-neighbor distance) most important in predicting hatching success, and the results differed among sites and species (Table 5). Elevation and date of nest-initiation were important in determining hatching success for Common Terns at all three sites analyzed, with higher elevation and later date of nest initiation improving hatching success.

DISCUSSION

Nest-site selection. Experimentally elevated plots were not preferentially selected for

at any of the shellpiles, or by any species. Contrary to expectations, Common Terns did not choose higher nest sites than were randomly available on shellpiles. While Common Terns did nest in high locations at at least two sites, the majority of their nests were at significant risk of flooding. Although elevation may not be the most critical factor in initial nest-site choice, it may have become more important later in the season as Common Terns renested at higher elevations after the 7 June floods (Fig. 3). Over 85% of Common Terns nested within 2 m of their nearest-neighbor, indicating that location of other nesting birds is also a strong selective force. The congregation of early nests in areas with American Oystercatcher nests further reinforces the potential for social attraction.

Black Skimmers primarily nested in the higher shell areas that were used by both Gull-billed Terns and Common Terns. They picked the area used by both tern species with shell as the primary substrate. Since Black Skimmers choose colony sites based on locations of Gull-billed and Common Tern colony sites (Erwin 1977; Pius and Leberg 1997), their nest-site selection is probably strongly influenced by the social stimulus of nesting near already-established tern nests at the shellpiles. However, because they nested somewhat later than terns at each site, they are presumably relegated to fewer choices than are terns, at least in the early nest-

Table 3. Extended.

Early nests		Late nests				
Failed	χ^2	Hatched	Failed	χ^2		
0.95 ± .01 (74) 1.16 ± .05 (3) 1.07 ± .01 (22)	14.3*** 0.7† 0.1†	1.02 ± .009 (56) 1.13 ± .01 (25) 1.07 ± .03 (4)	1.0 ± .02 (16) 1.2 ± .03 (5) 1.06 ± .02 (6)	2.7† 4.3* 0.1†		
$0.85 \pm .02 (44)$	11.3***	$1.08 \pm .02 (50)$	$1.14 \pm .04 (8)$	2.7†		
$0.89 \pm .03 (44)$	17.3***	$1.11 \pm .03 (47)$	1.18 ± .05 (19)	1.9†		
$1.34 \pm .02 (30)$	1.7†	$1.41 \pm .02 (29)$	$1.3 \pm .03 (24)$	6.2**		
		Sample size too small				

ing period. This may explain the lack of statistical differences in elevation we found for this species.

American Oystercatcher nest-site selection is probably based primarily on physical factors, since no other species are nesting on the shell-piles when American Oystercatchers begin choosing nest sites. Previous experience of nesting at the shellpiles may also play a strong role (Nol and Humphrey 1994).

The nest-site selection results do not seem to be a product of high spatial autocorrelation caused by birds nesting closely together; in fact, the shellpiles are highly variable and patchy habitats at fine scales. Points < 2 m away on the shellpiles often are located on different sub-

strates, have different exposures to open water, and can have differences >1 m in elevation. Vegetation is sparse and patchy with plants often located several meters from another plant. Nest-site selection varied among species and shellpiles, making it difficult to predict what areas of a shellpile will be used or avoided by nesting birds, though no sites appeared to be avoided due to presence of avian predators. Colony and site-specific factors appear to be important when examining nest-site selection.

Hatching success. Hatching success was not improved by experimentally elevating plots for any species, despite the apparent greater protection from flooding. We suspect this may have been caused simply by limited sample siz-

Table 4. Predation rates on all waterbird species at five shellpiles in coastal Virginia. There were no statistically significant differences between frequency of predation on early versus late nests^a. All Ruddy Turnstone predation occurred during the early season.

	Percentage of nests depredated (N)				
	All predation			Ruddy	
Site	Total	Early	Late	Turnstone predation	
Wire Narrows West	13 (39)	15 (26)	11 (13)	2 (7)	
Wire Narrows East	13 (22)	15 (15)	11 (7)	8 (13)	
Man and Boy	17 (29)	18 (19)	15 (10)	6 (11)	
South Conjers	3 (3)	3 (1)	3 (2)	1 (1)	
North Conjers	37 (10)	62 (8)	15 (2)	2 (7)	
Total	13 (103)	16 (71)	9 (32)	5 (39)	

 $^{^{\}rm a}$ Chi-square analysis, df = 1, all P > 0.4. Sample size was not large enough for analysis at South and North Conjers.

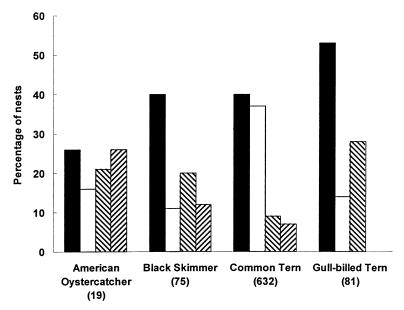


Fig. 3. Nest outcomes for each species of waterbird for all shellpiles combined (N). \blacksquare hatched; \square flooded; \boxtimes depredated; \boxtimes unknown.

es. Despite the limited success of the habitat manipulation experiment, the results indicate that elevation played an important role in hatching success on all the shellpiles. Common Tern nests at higher elevations had greater hatching success at all shellpiles except North Conjers. The 7 June flood had a strong effect on these results. At Wire Narrows and Man and Boy, early nests had improved hatching success at higher elevations. The hatching success of Common Terns at South Conjers was not affected by elevation in the early season, but only late, a reverse trend from that at other shellpiles. Thirty percent of late nests at South Conjers flooded, a much higher rate than any other shellpile (Fig. 2), and this may have affected the result. South Conjers is the smallest shellpile, and it is possible that birds were forced to renest in low-lying areas that flooded early because of competition for limited nesting sites. Buckley and Buckley (1980) suggest that the Common Tern's ability to adapt to salt-marsh nesting may be related to their ability to re-lay after losses to flooding. Late nests, many assumed to be renesters, accounted for between 43-57% of all Common Tern nests (depending on the shellpile), indicating that many birds renested after the 7 June flood. Black Skimmer and Gull-billed Tern hatching success was not affected by elevation; they also had low rates of flooding (Fig. 3), since they primarily nested in an area protected from floods.

Because of the unpredictable nature of flooding, the date of nest-initiation will be important to hatching success, even if the date is not consistent across different years. Late nests often have lower reproductive success than early nests (Spendelow 1982; Nisbet et al. 1984; Burger and Gochfeld 1990). In this study, however, hatching success improved in the late season, as late Common Tern nests had higher elevations (Rounds 2003) than did early nests and no major floods occurred.

Predation was, overall, not a major cause of nest failure at any of the shellpiles except North Conjers, where 62% of early nests were depredated. North Conjers had the smallest nesting colony, with a peak of only 13 nests. Ruddy Turnstones depredated over 70% of the first nests at Wire Narrows East (including 89% of Gull-billed Tern nests) when the colony had only 17 nests. Burger and Lesser (1979) found that smaller colonies had higher depredation rates, probably because fewer birds were present to mob predators. However, South Conjers, which was the second smallest colony but with the densest nesting (Rounds 2003), had the lowest depredation rates. Because nests were so

Table 5. Multiple logistic regressions using elevation, nest-initiation date, clutch size, and nearest-neighbor distance to explain hatching success in two species of waterbirds in coastal Virginia.

Site Species	Variable	N	Estimates of coefficients	SE	P
Wire Narrows West					
Common Tern		156			
	intercept		15.3	3.0	< 0.001
	elevation		-10.6	2.7	< 0.001
	nest-initiation date		-0.08	0.02	< 0.001
	clutch		-0.8	0.3	0.001
	nearest-neighbor		0.2	0.3	0.4
Gull-billed Tern		47			
	intercept		-20.3	10.7	0.06
	elevation		19.4	9.5	0.04
	nest-initiation date		0.03	0.05	0.5
	clutch		-2.4	1.1	0.03
	nearest-neighbor		0.003	1.5	0.99
Wire Narrows East					
Common Tern		105			
	intercept		-15.0	3.2	< 0.001
	elevation		10.3	2.7	< 0.001
	nest-initiation date		0.1	0.03	< 0.001
	clutch		0.8	0.5	0.6
	nearest-neighbor		-1.1	0.5	0.02
Man and Boy					
Common Tern		116			
	intercept		-10.7	2.3	< 0.001
	elevation		3.7	1.2	0.02
	nest-initiation date		0.08	0.02	< 0.001
	clutch		1.7	0.5	< 0.001
	nearest-neighbor		0.7	0.3	0.04
South Conjers					
Common Tern		72			
	intercept		7.4	3.6	0.04
	elevation		-4.4	2.1	0.03
	nest-initiation date		-0.03	0.02	0.15
	nearest-neighbor		-0.03	0.4	0.6
	cutch		0.2	0.4	0.9

dense over the whole shellpile, mobbing of predators was possibly more effective than at larger, more spaced colonies. Ruddy Turnstones had a significant impact on hatching success in early-season nests, especially for Gull-billed Terns at Wire Narrows East. All observations of Ruddy Turnstones at the shellpiles indicated that Gull-billed Terns, Common Terns, and Black Skimmers were extremely passive in their responses to Ruddy Turnstones. This observation is similar to others reported earlier (Crossin and Huber 1971; Parkes et al. 1971; Loftin and Sutton 1979; Brearey and Hilden 1985; Farraway et al. 1986).

Overall, hatching success was low on the

shellpiles. Hatching success for Common Terns in previous studies has ranged from 72% to 88% (Nisbet 1973; Nisbet and Welton 1984). Hatching success for Common Terns was just over 40% in our shellpile colonies. Eyler et al. (1999) found that hatching success for Gullbilled Terns was lower on marsh islands (54% hatched) than barrier island beaches (72% hatched). Overall hatching success for Gullbilled Terns was 54% in this study, although hatching success was very low (less than 15% hatched) at two of the three shellpiles used due to flooding and Ruddy Turnstone predation. Erwin (1977) found hatching success of Black Skimmers on barrier islands in Virginia to be

close to 80%, while Burger and Gochfeld (1990) found a lower hatching success rate of 54% on marsh islands in New Jersey. Only 45% of Black Skimmers nests on our shellpile sites hatched. Davis et al. (2001) found a hatching success of 12% for American Oystercatchers in North Carolina. At least 38% of American Oystercatcher nests hatched on the shellpiles; another 32% had unknown outcomes and could have hatched.

The multiple regression analysis revealed, across species and shellpiles, that elevation and date of nest initiation explain the most variation in hatching success. Clutch size and nearest-neighbor distance were significant contributors to the model at some shellpiles, but not all. Since date of nest initiation affected hatching success due to the early June flood, nest elevation appears to be the most important and consistent factor explaining hatching success.

Paradoxically, elevation did not appear to be the most important factor in nest-site selection, especially for Common Terns (Rounds 2003). The choice of a nest site by birds nesting on the shellpiles, therefore, appears to be uncoupled from the factor most important to reproductive success. The four species involved in this study historically nested primarily on barrier island beaches until human encroachment, habitat destruction, and invasion of mammalian predators drove them to seek alternative nesting sites (Gochfeld 1978; Erwin 1980; Erwin et al. 2001). The selective pressures determining nest-site selection may be based on selection on barrier island beaches, and thus may differ from what would be expected on lowlying marsh islands. The risk of flooding on barrier island beaches is generally lower relative to marsh islands (Burger and Gochfeld 1991; Eyler et al. 1999). Despite the failure of the experimentally elevated sites to attract nesting birds, the sites were protected from flooding.

Sea-level rise. If sea levels rise and if no new accumulation of shell on the piles occurs, the shellpiles will be completely inundated and unsuitable as colony sites. Although shellpiles are storm-deposited, oyster shell in Virginia bays has been a rapidly diminishing resource over the past century (M. Luckenbach, pers. comm.), so a source of shells to build up the shellpiles against higher sea levels will be lacking in the future. The number of floods over the marsh surface has increased in Virginia

since 1980 (Erwin et al., in press), and the number of birds using these sites is expected to decrease as increased flooding destroys low-lying nests. Many barrier island beaches have become unsuitable colony sites due to the widespread presence of mammalian predators. Erwin et al. (2001) reported that in 16 years, the number of suitable islands for nesting terns has decreased from 11 to nine, and colonies retracted from 23 to 13 sites; thus, nest sites appear to be a limiting resource. Total populations on the barrier islands have declined by >50% for three of the six species during 1977-1993 (Erwin et al. 2001). The results of this study demonstrate that rising sea levels pose a serious threat to breeding populations of seabirds on the Eastern Shore of Virginia, due to the low elevation of nests and the high frequency of flooding on shellpiles.

Management recommendations. Future management efforts may have more success if larger plots are used for shellpile elevation. Placing wrack and planting of vegetative cover at selected plots may encourage more birds, especially Common Terns, to nest at higher elevations. Creation of nest or colony sites free from predators and above rising tides may be necessary to maintain stable waterbird populations in coastal Virginia. Because the shellpiles are used annually and are more manageable than larger barrier islands in the face of rising seas, the effort to elevate the sites should be cost effective if it enhances habitat for three or four species whose populations are in jeopardy along the Virginia coast.

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