Nest-Site Selection and Hatching Success of Four Waterbird Species in Coastal Virginia

Rachel Ann Rounds
San Mateo, California

B.A., Williams College, 1995

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Abstract

Rising sea levels in the mid-Atlantic region pose a long-term threat to marshes and their avian inhabitants. Gull-billed Terns (*Sterna nilotica*), Common Terns (*S. hirundo*), Black Skimmers (*Rynchops niger*) and American Oystercatchers (*Haematopus palliatus*), species of concern in Virginia, nest on low shell 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 enhance habitat and reduce flooding, plots on five island shellpiles were experimentally elevated, and nest-site selection and hatching success assessed. Data on nest-site selection and hatching success were collected from May 1 to August 1, 2002. Common Terns chose nest sites on wrack on low-lying areas of the shellpiles exposed to open water. These nest sites left them vulnerable to floods, and 50% of Common Terns nests on the five sites were washed out during a June 7 flood. Gull-billed Terns and Black Skimmers primarily selected nest sites at high elevations on bare shell. Gull-billed Terns at Man & Boy were flooded due to low elevation nests, and Ruddy Turnstones predated 89% of Gull-billed Tern nests on Wire Narrows East. Black Skimmer nest-site selection may have been strongly influenced by nesting locations of terns. No species selected the elevated experimental plots preferentially, despite the protection they provided from flooding. Hatching success for all species was low, primarily because of the June 7 floods. Of the 5 physical factors analyzed, nest elevation had the strongest impact on a nests' probability of hatching. However, elevation did not appear to be the most important factor in determining a nest site. Small-scale manipulations to elevate nesting substrate yielded limited success as a management technique; suggestions are given for improving future design.

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Introduction

Gull-billed Terns (*Sterna nilotica*), Common Terns (*S. hirundo*), Black Skimmers (*Rynchops niger*), and American Oystercatchers (*Haematopus palliatus*) nest on storm-deposited shellpiles on salt marsh islands and on barrier island beaches in the barrier island-lagoon complex that characterizes the Eastern Shore of Virginia. Most shellpiles have low elevations, and may be subject to flooding due to spring high tides and storm surges during the breeding season (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, TNC, pers. comm.). Populations of 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 unpubl. data). American Oystercatcher populations have declined by more than 50% on Virginia barrier islands over the last 20 years (Davis et al. 2001). However, these numbers may not reflect population changes in all of Virginia, since marsh island populations are not included in these surveys.

One of the most significant threats to waterbirds in the Atlantic region is the decline in both the quantity and quality of habitat (Parnell et al. 1988, Erwin et al. in press). Because most of Virginia's barrier island habitats are protected, they have not experienced the same magnitude of human disturbance as other parts of the Atlantic Coast (Erwin 1980). However, over the last 25 years, the distribution of raccoons (*Procyon lotor*) and red foxes (*Vulpes vulpes*) has increased on Virginia barrier islands while the number of beach-nesting tern and skimmer colonies has decreased (Erwin et al. 2001). Shellpiles on salt marsh islands provide a haven from mammalian predators, but flooding during the breeding season may cause increased breeding failure (Burger and Lesser 1979, Eyler et al. 1999). In addition, loss of tidal marshes due to human encroachment has reduced available breeding and feeding habitat (Parnell et al. 1988). Because of growing mammalian predator populations on barrier islands, and frequent flooding on salt marsh shellpiles, safe nesting sites for waterbirds are limited in coastal Virginia (Erwin et al. 2001). The reduction in the quantity of suitable breeding habitat may continue if the predicted rise in sea level, due to global atmospheric warming, increases flooding of coastal areas (NAS 1987). A slight increase in sea level and/or higher frequency of storms could increase the frequency of flooding on shellpiles and barrier island beaches, and thus cause greater rates of breeding failure. Until recently the primary risk to marine birds was human habitat destruction (Brown 1991, Nettleship et al. 1994), but suitable breeding habitat for waterbirds may be even more restricted in the next decades as a rising sea encroaches on nesting sites, and mammalian predators continue to inhabit barrier islands beaches.

Because of habitat loss, expanding mammalian populations, and rising sea levels, management of waterbird breeding sites may become increasingly necessary. 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 project are 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 can improve reproductive success.

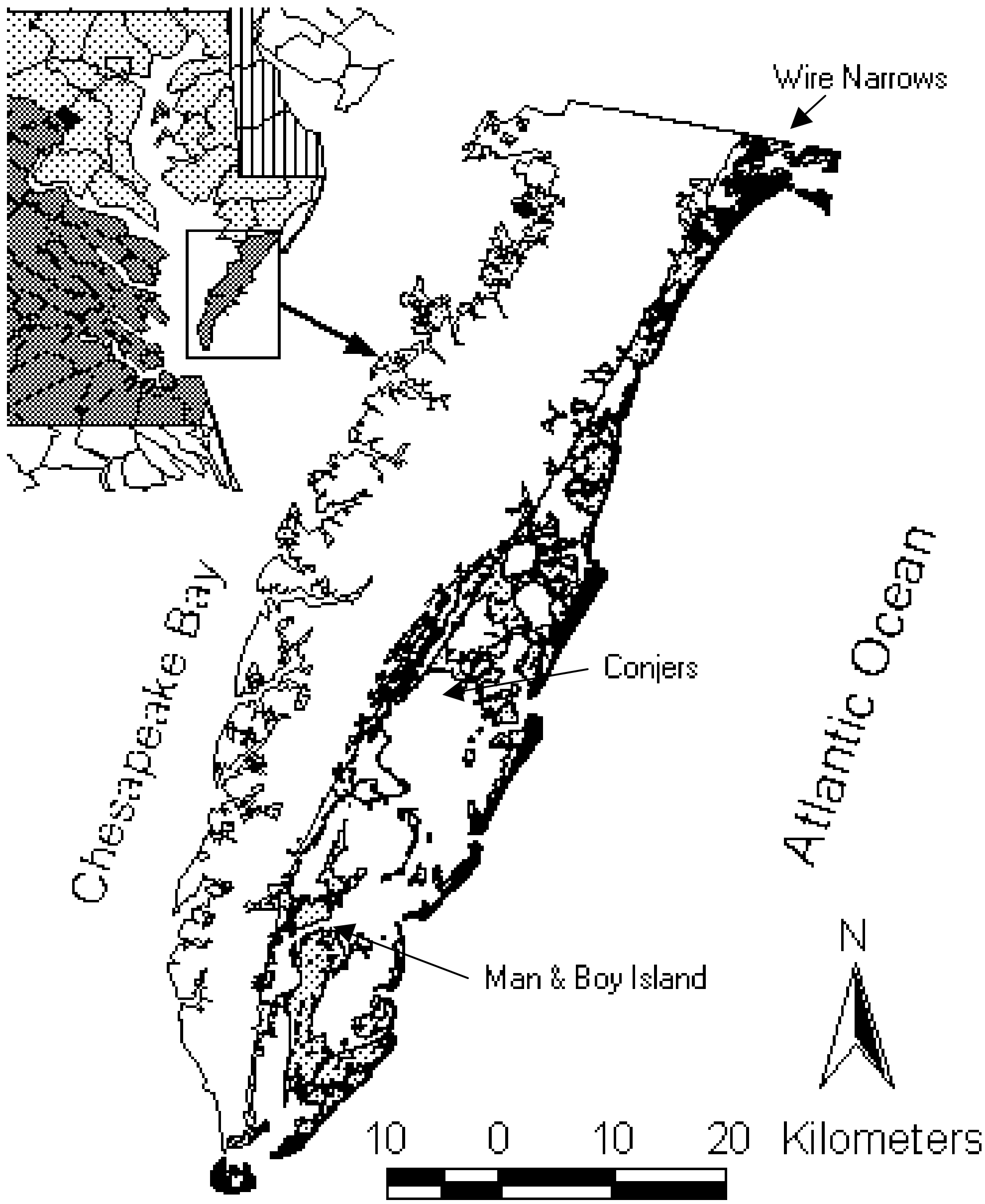
Study Site

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 marsh edges. The shellpiles have higher elevations than the surrounding marsh, and vegetation is present on lower-lying areas of some shellpiles. Wrack (dead vegetation mats of either *Spartina spp.* or *Zostera marina*) deposited by high tides and storms often rings 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). Although the highest portions of a shellpile may remain above water during high tides or storm surges, many other parts of the shellpile are inundated. The approximate edges of the high-water limit can be determined from the lines of recent wrack deposition.

Species Descriptions

Gull-billed Terns, Common Terns, and Black Skimmers frequently form mixed-species colonies along the Atlantic Coast on marsh, shellpile and beach habitats (Burger and Lesser 1978, Buckley and Buckley 1984, Humphrey 1990, Burger and Gochfeld 1991, Gochfeld and Burger 1994, Parnell et al. 1995). Black Skimmers often select colony sites based on the presence of other species, especially Common and Gull-billed Terns (Erwin 1977a, Pius and Leberg 1997). The American Oystercatcher is the only solitary nester that breeds on the shellpiles, though they will commonly nest near or in tern colonies (Burger 1985).

Figure 1. Map of the eastern shore of Virginia with locations of study shellpiles



Surveys of beach-nesting waterbirds on Virginia barrier islands from 1975-1994 found that Gull-billed Tern populations have declined by 95% (Williams et al. 1990, B. Williams unpubl. data). Gull-billed Terns are considered a threatened species by the Commonwealth of Virginia and the Virginia Natural Heritage Program ranks the species as G5/S2 meaning it is common throughout its range, but rare in Virginia (Byrd and Johnston 1991). Williams et al. (1990, B. Williams unpubl. data) found that Common Terns had decreased in coastal Virginia from 1975-1994 by 84% although some of the decrease may be related to a shift of more than 3000 breeding pairs to the Hampton Roads Bridge Tunnel (Erwin et al. 2001). Black Skimmer populations declined on Virginia barrier islands by 86% from 1975-1994 (Williams et al. 1990, B. Williams unpubl. data). The largest number of breeding pairs of American Oystercatchers on the Atlantic Coast is found in Virginia and this population increased from 1986 to 1993 by 300 pairs (Nol and Humphrey 1994). However, more recent data indicate that populations have declined by more than 50% from 1979 to 1999 on Virginia barrier islands (Davis et al. 2001). Threats to all species include loss of habitat to human encroachment, environmental contamination, human disturbance, predation, and localized flooding (Erwin 1980, Buckley and Buckley 1984, Williams et al. 1990, Byrd and Johnston 1991, Via et al.1992, Gochfeld and Burger 1994, Nol and Humphrey 1994, Erwin et al. 2001). Because of the declining population of these waterbird species, it is important to determine management methods to enhance breeding success at colony sites in Virginia and elsewhere.

Habitat and Nest-site Selection

Habitat selection can be defined as a series of decisions made by an individual resulting in the use of one habitat in preference to other available habitats (Jones 2001). Because habitat selection involves choices, it can be thought of as a behavioral process in which habitats are assessed and then selected for their influence on an individual's survival and fitness (Fretwell 1972, Jones 2001). Fretwell (1972) describes an "ideal free distribution" model for habitat selection in which individuals are free to select the habitat most suitable to them and to settle there. However, as the density of individuals in a habitat increases, the suitability of the habitat will decrease until a second habitat becomes more suitable and is selected. Eventually all habitats will have equal suitability. This model assumes that all individuals are free to enter a habitat and will select the habitat most suitable to them. In Virginia, the first level of nest-site selection will occur at the landscape scale (Burger 1985) as Gull-billed Terns, Common Terns, Black Skimmers, and American Oystercatchers select between nesting on barrier island beaches, shellpiles on salt marsh islands, or on wrack or *Spartina* on the marsh surface. The second level of nest-site selection involves choosing a certain shellpile, the third choosing a territory, and the fourth selecting a nest site within it (Burger 1985).

Nest-site selection is of primary importance for the reproductive success of a breeding pair. The selection of a nest site is influenced by physical factors, including elevation, substrate, exposure, slope and aspect, and biological factors, including presence of conspecifics and heterospecifics, vulnerability to predation, and previous experience (Buckley and Buckley 1980). These factors combine to define the nesting habitat chosen by a bird.

The elevation of a nest site is particularly important on shellpiles that are subject to flooding. American Oystercatchers have been shown to prefer higher nest sites (Lauro and Burger 1989), as have Gull-billed Terns (Clapp et al. 1983). American Oystercatchers also used elevated platforms for nesting in Virginia (Nol and Humphrey 1994). In an experiment using artificially constructed wrack-mats, 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), examining nest-site selection with regard to elevation will be an important management component of research. I expect that since higher nest sites will provide greater protection against flooding and nest failure, species will select higher nest sites than are randomly available on the shellpile. Since early nesters have first choice of quality nest sites, it is expected they will choose sites of higher elevations. For example, since American Oystercatchers arrive earliest in the spring, they should chose the highest sites.

Choice of substrate on the shellpiles is limited to dense shell or tidally-deposited wrack, or a combination of the two. Nests of Gull-billed Terns (Parnell et al. 1995), Common Terns (Burger and Lesser 1978, Burger and Lesser 1979), Black Skimmers (Gochfeld and Burger 1994), and American Oystercatchers (Nol and Humphrey 1994) have all been found on wrack and shell. Nests on wrack can provide protection from flooding by acting as a floating raft, unless wind-driven waves break it apart (Burger and Lesser 1978, Lauro and Burger 1989, Gochfeld and Burger 1994). Substrate can also provide camouflage for eggs and chicks (Burger and Lesser 1978, Kotliar and Burger 1986, Mallach and Leberg 1998). Exposure of a nest site to sun, wind, and waves will also affect nest-site selection. The presence of vegetation near a nest site can affect exposure to sun and provide cover for adults, eggs, and chicks. Once chicks are old enough to move around, proximity to shade and shelter may improve chances of survival, and thus the area surrounding a nest may be an important factor in nest-site selection. However, thick vegetative cover can reduce visibility (Leberg et al. 1995). Black Skimmers had less vegetative cover than Common Terns around their nests in New York (Gochfeld 1978) and preferred areas with less than 30% cover (Gochfeld and Burger 1994). Gull-billed Terns prefer nest sites with sparse vegetation that are near areas with denser vegetation (Sears 1978). Common Terns on beaches in New York nested in areas with 10-25% vegetation cover, and avoided overgrown areas (Burger and Gochfeld, 1991). The exposure of a shellpile slope to wind or storm-driven waves may also influence nest-site selection. Nests on slopes facing an open lagoon will have a greater chance of flooding than will nests on marsh-facing slopes. Changes in wind direction may also affect which side of the shellpile is flooded (Burger and Lesser 1979, Burger 1982). To enhance success, birds are be expected to choose nest sites that minimize exposure to wind and waves, and provide protection for eggs and chicks (either through substrate or vegetation).

In addition to physical factors, social factors are often important in nest-site selection. Competition for nest space in colonial-nesting species can be very intense (Buckley and Buckley 1980), especially when nest sites are limited, such as on shellpiles. Oystercatchers typically arrive on last year's territory in late March/early April (Nol and Humphrey 1994) and lay their first clutches during the first week of April, with a peak in mid-April (Nol and Humphrey 1994). Gull-billed Terns arrive in late April to early May

(Byrd and Johnston 1991) with nest building beginning 5 to 25 days afterwards and egg-laying in mid-May to early June (Parnell et al. 1995). Common Terns also arrive in late April/early May, begin establishing territories the first two weeks in May, and lay eggs around May 15 (Erwin 1979), but usually slightly later than Gull-billed Terns (R.M. Erwin, pers. obs.). Black Skimmers arrive from late April to early May (Erwin 1979), with peak egg-laying the third week of May (Erwin 1979). Black skimmers are usually the last of these species to lay eggs (B.R. Truitt, TNC; R.M. Erwin, pers. obs.), but may renest as late as August in Virginia (B.R. Truitt, unpubl. data).

As the first species to arrive and establish nests, American Oystercatchers have the broadest range of nest sites available to them. Their choice of prime, high-elevation nest sites may limit species arriving later in the season from using these sites. Aggressive and territorial behavior from birds (especially large-bodied species) with established territories will further affect nest-site selection of later-arriving birds. Fretwell (1972) described an “ideal despotic distribution,” in contrast to the earlier-mentioned ideal-free distribution, in which aggressive behavior from an individual with an established territory deters a later-arriving bird from settling. The suitability of this habitat will now not only be density-dependent but also dependent on the social dominance of already-settled heterospecific individuals (Fretwell 1972). The sequence of arrival at shellpiles, and the behavior of the early-arriving birds, may influence the final distribution of nesting birds, and overall species nest-site quality (e.g. higher elevations). Common Terns are known to be the most aggressive of the four species (Erwin 1979), and this may influence the frequency, intensity, and outcome of their aggressive interactions. Species size may also influence the outcomes of aggressive encounters (American Oystercatcher, Black

Skimmer, Gull-billed Tern, Common Tern, ranking largest to smallest). In addition, aggression may be density-dependent.

Selection of a nest site within the colony is also an important factor in nest-site selection. Aggressive territorial behavior could also serve to space individuals within a habitat (Fretwell 1972). Solitary American Oystercatcher nests were spaced an average of 124 to 190 m apart, depending on the habitat (Nol and Humphrey 1994). Nearest-neighbor distances for Gull-billed Terns ranged from 2 to 92 m in Denmark, with an average of 22.4 ± 14.3 m (Moller 1981) and 4 to 16.5 m in North Carolina (Sears 1978). Distances between Gull-billed Tern and Common Tern nests ranged from 5 to 10 m, and Gull-billed Tern-Black Skimmer nests from 2.7 to 8.5 m (Sears 1978). Burger and Lesser (1978) found that Common Terns nested a mean distance of 0.8 to 4.8 m apart on New Jersey salt marshes, depending on substrate, size of island, and colony space, while Erwin (1977b) found inter-nest distances of 1.6 ± 0.49 m on Virginia barrier islands. Pius and Leberg (1997) reported that Black Skimmers nest, on average, 1.68 m from other Black Skimmers, and 1.53 m from Gull-billed Terns in Louisiana. Mean nearest-neighbor distance for Black Skimmers in salt marsh colonies ranged from 1.0 to 5.3 m in New Jersey (Gochfeld and Burger 1994). These distances, especially for Gull-billed Terns, are greater than those I observed on the shellpiles in 2001, where nests were often less than 1.0 m apart in densely packed clusters of 8-10 Gull-billed Tern nests. Small shellpile area with limited nesting sites probably causes nest densities to be higher on shellpiles than on other, larger sites.

Black Skimmers commonly nest among Common Terns and Gull-billed Terns in Virginia (Erwin 1977b, Erwin 1979). Most of the nest distribution within Common Tern-

Black Skimmer colonies can be attributed to differences in microhabitat preferences between the two species (Erwin 1979). Common Terns nested near vegetation while Black Skimmers nested in open sand patches on barrier islands (Erwin 1979). Skimmer nests are often clustered within the colony of terns they are nesting with (Burger and Gochfeld 1990). On Man & Boy Island in 2001 some Common Tern nests were located within the area occupied primarily by Gull-billed Terns, but most nests were segregated by species (R. Rounds, pers. obs.). In addition, Black Skimmer nests were interspersed among Common Tern and Gull-billed Tern nests on North Conjers in 2001 (R. Rounds, pers. obs.).

Vulnerability to predation may also influence nest-site selection. Black Skimmers will abandon colonies after unsuccessful breeding seasons due to high predation rates (Burger 1982). Predation on marsh islands is usually limited to avian predators such as Herring (*Larus argentatus*), Greater Black-backed (*L. marinus*) and Laughing Gulls (*L. atricilla*), American Oystercatchers, Ruddy Turnstones (*Arenaria interpres)*, and Great-horned Owls (*Bubo virginianus)* because frequent flooding of the low-lying islands deters mammalian predators (Burger and Lesser 1979). Colony-site selection may be affected by the presence of predators, while nest-site selection will be a function of choosing a "safe" site from predators and other potentially aggressive nesting associates, whether at the edge of a colony near vegetative cover, or in the center of the colony.

The distribution of nests on shellpiles is likely a function of the interaction between physical and biological factors. Competition for territories is both inter- and intraspecific, with birds arriving first at the site having an advantage in nest-site selection. Prime nest sites will be occupied first, with later nests filling in the empty space. As the season progresses, nearest-neighbor distances will decrease, as nest density increases (Burger and Lesser 1979), and thus the spatial patterns of nests on the shellpile will change.

Hatching Success

Because of the high flooding risk to shellpile nesting, the physical location of the nest on the shellpile is expected to have a strong influence on nest success. First, the elevation of a nest can have a direct effect on nest success. The higher the nest, the less likely it will be inundated and destroyed during flooding. Second, the exposure of the shellpile to tides and waves will affect nest success. In addition, since date of nest initiation may indirectly affect nest elevation, it may have an effect on nest success as well. Substrate and vegetation could also influence hatching success by providing better cover from predators or the sun.

Biological and social factors that are involved in nest-site selection can also directly influence hatching success. The date of nest initiation, which may influence nest elevation, is also a function of parental age and experience, food resources, weather and tidal regimes (Nisbet 1977, Burger and Gochfeld 1991). Clutch size may also reflect parental quality as it reflects the amount of energy invested in an egg (Nisbet 1977, Nisbet 1978), as well as being an indicator of resource availability (Burger and Gochfeld 1991). The spacing of nests within the colony is a function of nest-site selection, and may also influence reproductive success. Within a colony, centrally located nests may have increased nesting success because they are buffered from predators by peripheral nests (Buckley and Buckley 1980). Burger and Gochfeld (1990) found that centrally located Black Skimmer nests in New Jersey had higher hatching success, were closer to Common

Tern nests, and had larger clutches than nests closer to edges. However, the opposite was found for Common Terns in New Jersey, perhaps because nests at the edge of a colony were closer to sheltering vegetation (Burger and Gochfeld 1990). Since the shellpiles in Virginia are usually linear, colonies tend to have more edge and little center.

Ground-nesting birds are vulnerable to predation and therefore nest spacing and presence of concealing vegetation are important factors influencing reproductive success (Buckley and Buckley 1980). Laughing Gulls nest in close proximity to the shellpile colonies at Wire Narrows and have been known to prey upon Common Tern chick and eggs (Burger and Gochfeld 1991). At one of my colony sites, Ruddy Turnstones were observed preying upon Gull-billed Terns in 1995 during several visits (R.M. Erwin, pers. observ.) and are well-known egg predators that have predated 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). Predation rates also can vary throughout the breeding season, affecting early and late nests differently (Shealer and Kress 1991). Avian predators are expected to cause some nest failure, and the nest-initiation date and spatial location of the nest will influence its probability of predation.

Sea Level Rise

Sea levels along the Atlantic Coast of the United States are currently predicted to rise 46 cm by 2100 (IPCC 1996). This could have devastating effects on the amount of habitat available to nesting birds that is safe from flooding and also on area of habitat available to nesting colonies. Flood tides are likely to destroy some nests each year; however, the extent and timing of the flood damage will be different from season to season depending on wind and storm conditions. As sea levels rise, it can be expected that the number of floods will increase each breeding season, along with the number of nests lost during each flood tide. Tide data from Wachapreague, Virginia from 1980 to 2001 suggest a significant increase in frequency of flooding of marshes during the May-July period (R.M. Erwin, unpubl. data).

Research Questions

To make the presentation more organized, I have divided the series of questions into 2 major areas: nest-site selection and hatching success.

Nest-site Selection

1. How does elevation affect nest-site selection?
    a. Do species nest on experimental plots at a higher density than on control plots?
    b. Do species select higher nest sites than what is generally available on the shellpile?
    c. Are there differences in the elevations of early versus late season nests?
2. How do substrate and exposure affect nest-site selection?
    a. Which substrate(s) does each species prefer for nesting?
    b. What level of exposure to open water does each species prefer at a nest site?
    c. Does the choice of substrate and exposure differ from what is generally available on the shellpile?
    d. Does the choice of substrate and exposure differ between early- and late-season nests?
    e. Do substrates and exposure levels differ in elevation?

3. How does the presence of vegetation influence each species nest-site selection?
4. How does distance to the nearest-neighbor influence nest-site selection?
    a. Are nearest-neighbor distances different between conspecifics and heterospecifics?
    b. Does nearest-neighbor distance vary between early- and late-season nests?
    c. How densely does each species nest?
    d. Does the density of nests change between early- and late-season nests?
5. Does behavioral aggression during nest-site selection affect the number of nests on experimental plots?

Hatching Success

6. How does elevation affect hatching success?
    a. Do successful (hatched) nests have higher elevations than unsuccessful nests?
    b. Does elevation affect hatching success in both early- and late-season nests?
    c. Does flooding frequency vary between early- and late-season nests?
7. Do substrate and exposure affect hatching success?
8. Does presence of vegetation near a nest affect hatching success?
9. Does date of nest initiation affect hatching success?
10. Does clutch size vary between early- and late-season nests?
11. Does clutch size affect hatching success?
12. How does predation affect hatching success?
    a. Are there differences in predation rates among shellpiles?

b. Are there differences in predation rates between early- and late-season nests?

c. Does nearest-neighbor distance affect predation rates?

13. Does nearest-neighbor distance affect hatching success?

14. Do biological or physical factors explain the most variation in hatching success?

Methods

Experimental Elevation of Plots (Question 1a)

From March 11-14, 2002, before the focal species arrived at the shellpiles to nest, plots on the shellpiles were experimentally elevated. We created 6 sets of paired plots (one elevated, one control) at 4 of the shellpiles, and 4 paired plots at the smaller South Conjers shellpile. The location of the paired plots was randomly determined by laying a meter tape down along the long axis of the shellpile, and using a random number tape 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 similar to its paired control plot, including addition of wrack where necessary. We attempted to make experimental plots 15-20 cm higher than control plots. Fine shell was added to the tops of elevated plots to mimic the natural shellpile features. Each plot was 2 m by 2 m. Based on previous experience at the shellpiles, we believed this area was sufficient for at least 4 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. Stakes were put into the shellpile at the four corners of each plot. All experimental plots were elevated using oyster shell from lower or out-lying areas of the shellpile not used by nesting birds. At

Wire Narrows West two plots were partly elevated by laying a layer of wrack at the bottom and covering it with shell. A third plot was elevated using a pallet and covering it with shell. I measured the elevations of control and elevated plots using a laser level. If the plot was located along a ridge, multiple points were taken at different elevations. The increase in elevation on experimental plots was not high enough to produce changes in predation rates, or influence microclimate or other factors that might affect nest-site selection.

I set up six paired plots at Wire Narrows West. Three plots were located in an area used by nesting Gull-billed and Common Terns in 2001 and three were located in an area that had fewer, or no, nests in 2001. I also set up six paired plots at Wire Narrows East. Three paired-plots were in areas high nest density in 2001, and three in areas of low nest density. I created six paired plots at North Conjers; however, lack of knowledge of previous nesting patterns precluded identifying areas as used or unused. Only 4 paired plots were established on South Conjers due to the small size of the shellpile, and no areas of the shellpile were established as previously used or unused. I also created six paired plots at Man & Boy. Three of the paired plots were in an area of high nest density in 2001, and three in areas with fewer, or no, nests.

Random Points (Questions 1b, 2a, 2b)

I located twenty-five random points on each shellpile and elevation, substrate, slope and exposure were recorded for each point. Random points were located by laying a measuring tape down the long axis of the shellpile and determining distance to the point from a random number table. A second random distance (0-10 m) was selected to go either left or right to locate the point. I measured the elevation of random points using a laser level. Substrate was limited to oyster shell, wrack, or a combination of the two. Slope and exposure were recorded using an index combining the two variables (Table 1). Exposure was based on exposure to waves. Areas of the shellpile facing an expanse of marsh were “protected,” those facing open water were “exposed,” while those on ridges or in the middle of the shellpile were “neutral.” In addition, if a random point was located in a plot this was recorded, along with whether the point fell within an area of high, low, or no nesting density from 2001.

Table 1. Categories used to describe slope and exposure on shellpile sites.

Slope	**Exposure to Waves**
flat	exposed
flat	protected
flat	neutral
sloped	exposed
sloped	protected
sloped	neutral

Nest Monitoring (all questions)

I monitored the shellpiles twice a week for nesting activity from May 1 to July 31. To minimize disturbance to nesting birds, I visited the shellpiles for less than 30 minutes, and to the extent possible, visited during the cooler hours of early morning or evening. After clutches were initiated, I marked nests with 25 cm nails hammered into the shellpile within 6-8 cm of the nest scrape. All nests on the shellpiles were monitored. I tied a metal tag with nest number and species to the nail. I recorded the following during each visit: species, content of the nest, substrate, slope/exposure, and presence of nearby vegetation when the nest was first found. The status of each nest was assessed during each subsequent visit. If a nest scrape was empty, I 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 predated. Eggs were also routinely felt for temperature and signs of abandonment. I assigned new nest numbers for renesting attempts in a previously used scrape. I monitored nests only until hatching, because determining fledging success is logistically difficult without using enclosures (Eyler et al. 1999).

I recorded the date of nest initiation (first egg laid) 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 (incubation length averages 22 days in Gull-billed Terns [Parnell et al. 1995], 21 days in Common Terns [Parnell and Soots, 1979], 23 in Black Skimmers [Gochfeld and Burger 1994], and 26 in American Oystercatchers [Nol and Humphrey 1994]). If a nest was found with a full clutch and subsequently failed, I estimated the dates of nest initiation from the dates of previous nest visits. At the end of the season, the elevation of every nest was recorded with a theodolite total station unit.

Tide Gauges

I set up temporary tide gauges at each shellpile to determine heights of spring high-tides and storm waves. A piece of 120 cm long, 5 cm wide PVC with holes drilled in the sides was inserted into the marsh near the shellpile. I added ground cork to the PVC and the level of the cork after high tides was recorded within 1-2 days of high-water events. In addition, I recorded the elevation of each tide gauge using a theodolite total station unit.

Behavioral Observations

To evaluate the role of social interactions, I observed bird interactions at Wire Narrows West and East during the early stages of the breeding season from a platform located 150 meters from Wire Narrows West and 190 meters from Wire Narrows East. The presence of an observer on the platform at this distance did not disturb the birds. I used a spotting scope, binoculars, and a cassette recorder for observations. I began observations of the shellpiles on May 1, 2002 and continued until May 29, 2002. I discontinued observations when the majority of birds had established nests and territories.

I used focal-animal sampling (Altmann, 1974) for the behavioral observations. I randomly selected an individual bird and observed it for as long as the bird was visible, for a maximum of 10 minutes per sample. I discarded all observations of less than 1 minute. I recorded all aggressive behaviors observed during this period involving the focal animal, including behaviors initiated and received by the focal bird. Aggression was ranked on 5 levels ranging from no aggression to aerial stoop attack. I recorded the species of each bird involved in an aggressive interaction, along with the approximate stage of nesting of the majority of individuals of each species (pre-egg laying, egg laying, incubating, hatch) and the outcome of the interaction. At the beginning and end of each sampling session, a census of all the birds within 2 and 5 m of the focal animal was conducted. If the focal animal was located within either an experimental or control plot then the number of birds within the plot and within 5 m of the focal animal was recorded.

Due to the low nesting density in areas visible from the platform on Wire Narrows West and East, I also used focal-area sampling (Altmann 1974). An area of the shellpile about 10 m in length was observed continuously for 30 minutes. At ten-minute intervals I recorded all birds in the observation area. During this time all aggressive interactions between species were recorded as described above.

Data Analysis Methods

Statistical

I conducted a power analysis (O'Brien 1998) using UnifyPow and SAS to determine if 25 random points were enough for t-test comparisons between random point elevation and nest elevation. I used chi-square analysis on contingency tables to test for many of the analyses in order to determine if observed frequencies matched expected frequencies. I used contingency tables for all analyses of nest-site selection and hatching success involving substrate, exposure, and vegetation. I also used contingency tables to analyze data involving hatching success and nest-initiation date, flooding, and predation. Contingency tables were used to test for goodness-of-fit for nest-site selection data and independence for hatching success data. In order to test for differences between means, T-test and Analysis of Variance (ANOVA) were used to analyze some of the elevation, clutch-size, and nearest-neighbor data. Because I was interested in what factors explained hatching success, I used logistic regressions to examine if elevation, clutch size, lay date, and nearest-neighbor distance influenced hatching success. All data analysis was performed using the SAS statistical package (SAS 1999) except nearest-neighbor distances which were calculated using the Distances function in SPSS (SPSS 2002).

Description of Variables used in Analysis

Substrate: Substrate was divided into shell, wrack (washed up dead vegetation) and shell-wrack. Shell-wrack indicates that nest substrate was a combination of shell and wrack.

Slope-Exposure Index: Because of small sample sizes, I combined the flat and slope categories into exposed, protected, and neutral. Observation in the field made it clear that exposure to flooding was a more important variable to nest success than flat or sloped. In addition, the small number of nests on protected sites made analysis difficult so these nests were combined with either neutral or exposed sites depending individually on their location.

Vegetation: I recorded "vegetated" nests as being those within 30 cm of a patch of vegetation of any type, regardless of density.

Clutch size: The clutch size for each nest used in the analysis was total number of eggs in each nest. Nests that failed before full clutch size was reached were excluded from the analysis.

Lay Date: Lay date was determined from the hatching date and the date the nest was first observed. May 1 was chosen as day 1 since all nests, (with the exception of American Oystercatchers), were initiated after this date.

Early vs. Late nests: All nests initiated after June 7 were considered "late" nests. June 7-12 was the week of a large early season flood that destroyed 47% of all nests. Soon after this flooding, a new wave of nest-initiation began of "late" nests.

Nearest-neighbor: The shortest distance from the focal nest to a neighboring nest. Because some nest-stakes were lost in floods, the location of each nest could not be determined. These nests were left out of all nearest-neighbor analysis, and so the nearest-neighbor distance may be slightly overestimated.

Areas: The area of "used habitat" was calculated in ArcView by tracing the outer edges of the colony, or focal nests. The more inclusive "available habitat" is the area of the whole shellpile, including areas used by nesting birds. I calculated nesting density using both "used" and "available" areas.

Nest Outcome: I grouped nests as either "hatched" (= 1 egg) or "not hatched" for analysis. If one egg of the clutch hatched then the nest was considered successful for analysis purposes. If I found a dead chick on the next visit, this nest was still classified as "hatched." I considered nests whose eggs survived more than 20 days to be successful, even if their eggs or chicks were not found on the next visit. Most nest predation occurs in the first 2 weeks of nesting (Erwin and Smith 1985, Eyler et al. 1999). Some of these nests also showed signs of chick presence (fecal matter, flattened wrack) indicating hatching. Nests whose outcome could not be determined were listed as unknown, and excluded from analysis.

Predation: I considered a nest predated if evidence of predation (broken eggs, yolk in nest) was found at the nest scrape or in the nearby vicinity. In addition, eggs that disappeared before they should have hatched were considered predated.

Flooding: Because a new wrack line is deposited after a flood, determining nest flooding was unequivocal. The new wrack usually contained many of the eggs that were washed out of their scrapes. Indications of flooding also included deposition of new shell over the nest scrape, and flattening of the scrape by wave action. I relocated many nests by digging through shell and wrack until the nest stake was located.

Abandoned nests: Nests were considered abandoned when eggs were felt to be cold to the touch, or when they were present more than 5 days beyond the expected hatch date (30 days for Common Terns).

GIS

I used ArcView 3.2 (ESRI 2002) and ArcInfo (ESRI 2002) to analyze Global Positioning System (GPS) data collected from the GPS survey units.

Tides

The tide data used for this research was provided by the Virginia Institute of Marine Science (VIMS 2002) and NOAA websites (NOAA 2002) for Wachapreague, Virginia.

Results

Nest-Site Selection

Physical Factors

Experimental Plots (Question 1a)

South Conjers had the highest percentage of nests on elevated plots (8%) compared to just 2% at Wire Narrows East (Table 2). In addition, 10% of late nests at Wire Narrows West were on elevated plots. At all five shellpiles, nesting birds did not select experimental plots as nest sites at different frequencies than compared to controls (Table 2). The density of nests on experimental plots was lower than on the used area of the shellpile as a whole except at Wire Narrows West. At Wire Narrows West the density of nests on experimental plots was 2.38 nests/m^2 while the overall density on the used area of the shellpile was 0.9 nests/m^2.

Elevation (Question 1b&c)

The power analysis found that with a sample size of 25 random points and 50 nests, a standard deviation for elevation of 0.122 m (based on the random point standard deviation), and a difference in elevation of 0.1 m, the power of the test was over 0.9. Because sample sizes were larger, and standard deviations lower, than used in the power analysis, the power to detect differences between random points and nests elevations was high.

There were shellpile and species differences in nest elevations (Figures 2-3, Table 3, Appendix 3). Common Tern nests at both Wire Narrows shellpiles were significantly lower than random points, while at the two Conjers shellpiles Common Tern nests were significantly higher than random points. At 3 shellpiles late Common Tern nests were significantly higher than early nests (Figure 3). Gull-billed Tern nests were significantly higher than random points at one colony, and lower at another colony, although not significantly. Black Skimmer nests were not different in elevation than random points. American Oystercatcher nests were, on average, higher than random points at all sites, although not significantly (Figure 2).

Substrate and Exposure (Question 2)

Species differed in their utilization of substrate and exposure of nest to open water, and site differences existed as well (Figure 4, Table 4-5). At all sites, nest substrates (Table 4) and exposures (Table 5) were chosen differently from that available. Overall, Common Terns preferred wrack on exposed slopes (39% of all nests), Gull-billed Terns and Black Skimmers selected shell on neutral slopes (62% and 61% of all nests, respectively), and American Oystercatchers preferred shell on neutral slopes (58% of all nests). At Wire Narrows East and South Conjers, the number of Common Tern nests on wrack decreased over the season (Appendix 6). At Wire Narrows East and Man & Boy the number of Common Tern nests on exposed slopes decreased, and on neutral slopes increased, between early and late nests (Appendix 7). For all shellpiles except North Conjers, the elevation of neutral nests was higher than that of nests on exposed slopes (Table 6), and at 3 shellpiles, shell nests were significantly higher than nests on either other substrate (Table 7).

Vegetation (Question 3)

No vegetation was present on North Conjers or Man & Boy shellpiles. Only Gull-billed Terns at Wire Narrows West nested near vegetation at a high frequency (70% of nests, Table 8). Gull-billed Tern and Common Tern nests near vegetation were significantly lower than were nests remote from vegetation (Table 8).

Biological Factors

Nearest-Neighbor Distance (Question 4a&b)

The average distance from each species nest to its nearest-neighbor illustrates major species and site differences (Table 9). The average distance from each species to its nearest-neighbor of each species is shown in detail in Appendix 8. In assessing seasonal effects (question 4b), late Common Tern nests were closer together than early nests at all sites but Man & Boy (where nests were the same distance apart, Table 9). Both Black Skimmer and Gull-billed Tern late nests were closer to nearest-neighbors than early nests.

Density and Area (Question 4c&d)

The area of each shellpile and the density of nests in both used and available habitats are shown in Table 10. The density of Common Tern nests in used areas ranged from 0.47 nests/m^2 at North Conjers to 0.9 nests/m^2 at South Conjers, and densities of nests also varied between early and late nests (Table 11). Gull-billed Tern nest density ranged from 0.7 nests/m^2 to 1.9 nests/m^2 and also varied between early and late nests (Table 11).

Behavioral Observations (Question 5)

A total of 30 hours of behavioral observations were conducted. The observations were limited since most of the early-nesting terns did not establish nests in areas visible from the observation platform. While all 6 plots on Wire Narrows West were visible, and 3 plots on Wire Narrows East were visible, very few birds nested on these plots, thus the number of focal animals was limited. Further, nesting density was low in most of these areas and that may have limited interspecific aggressive interactions. Once focal area sampling was used, more birds were included in the observations; however due to the limited area of the visible shellpile used by nesting birds, repeated observations probably were made of the same nesting pairs (although, without marked birds, this is speculative). However, qualitative data were collected that shed some light on behavioral interactions during nest-site selection, and how these processes may have affected nest-site selection on experimental plots.

The number of interspecific aggressive interactions I observed illustrated species asymmetries (Table 12). All six of the occurrences of American Oystercatchers chasing Black Skimmers occurred at the time of hatching of the focal American Oystercatcher's nest. The Black Skimmers were all within 10 m of the nest, and the American Oystercatcher pair repeatedly chased the birds from the area. Four days later, on my next visit to the shellpile, many Common Tern, Gull-billed Tern, and Black Skimmer nests were found in the area of the Oystercatcher nest. In fact a Common Tern pair was using the same scrape as the Oystercatcher nest. The aggressive behavior of the American

Oystercatchers, therefore, appeared to have no lasting impact on nest-site selection of the other species using the shellpile.

Seventeen of the aggressive interactions initiated by Gull-billed Terns towards Black Skimmers were from a pair of Gull-billed Terns nesting on experimental plot 3E on Wire Narrows West. The aggressive behaviors were first observed on May 25 and eggs were first found in this nest on May 27. Thirteen of the aggressive interactions resulted in Black Skimmers leaving the area (Table 12). However, despite the territorial aggression exhibited by the Gull-billed Tern pair, on June 4 a Black Skimmer nest was found on plot 3E in the same place the Black Skimmer pair had occupied earlier. The Gull-billed Tern nest was still active at this time. By June 18 there were 3 Gull-billed Tern and 3 Black Skimmer nests on plot 3E. The aggressive behavior of the first Gull-billed Tern nest initiated on plot 3E did not affect future use of the plot by pairs of either species.

Common Tern nests on Wire Narrows East and West were primarily found in low-lying vegetated areas and were not visible from the observation platform. However, one area used by both Gull-billed Terns and Common Terns was visible. Very few aggressive interactions between the two species were observed (Table 12) and both species nested in close proximity in this area.

Hatching Success

The summary of hatching success indicates some species differences (Figure 5 and Appendices 9-13).

<u>Physical Factors</u>

Elevation (Question 6)

Elevation had a significant positive effect on hatching success for Common Terns at all shellpiles except North Conjers (Table 13). At 3 shellpiles, however, hatching success was improved only in early nests (Table 14). Hatching success improved with decreasing elevation for late season Gull-billed Terns at Wire Narrows West (Table 14). Hatching success of Black Skimmers was not affected by nest elevation.

For all shellpiles, except North Conjers, significantly more early nests flooded than late nests because of the high-water period of June 7, 2002 (Figure 6). For all the shellpiles (excluding North Conjers) there was a significant difference ($P<0.001$) between the elevations of flooded nests and non-flooded failed nests. The elevations of failed nests that did not flood were not significantly different from the elevations of nests that hatched. This indicates that elevation only affects nest success with respect to flooding frequency and does not affect other factors that might influence a nests' outcome.

Substrate and Exposure (Question 7)

There was no significant difference in hatching success between nests on shell, wrack, or shell-wrack at Wire Narrows West, South Conjers, or North Conjers (Table 15). At Wire Narrows East and Man & Boy hatching success was highest on shell-wrack and lowest on wrack. All sites yielded higher hatching success for Common Terns and Gull-billed Terns on neutral sites than exposed sites (Table 16).

Vegetation (Question 8)

Hatching success is significantly lower at nest-sites near vegetation for Common Terns at both Wire Narrows sites, but higher for Gull-billed Terns at Wire Narrows West (Table 17).

Biological Factors

Nest-Initiation Date (Question 9)

Peak nest-initiation dates for each species are shown in Figures 7-9. Common Terns had higher hatching success later in the season at all sites (Table 18). There were no seasonal differences in Gull-billed Terns or Black Skimmer hatching success.

Clutch Size (Question 10&11)

Average clutch size for early and late nests did not show consistent seasonal declines (Table 19). Black Skimmers had significantly smaller clutch sizes in later nests; I found 4 and 5-egg clutches early in the summer, but none late. Common Terns at Wire Narrows East, Man & Boy, and South Conjers also had significantly smaller clutch sizes in later nests.

The effect of clutch size on hatching success revealed that, for all species, as clutch size increased, hatching success increased (Fig. 10). At four sites, Common Tern nests with 2-egg clutches had the highest hatching success.

Predation (Question 12)

At all five shellpiles there were no statistically significant differences in the frequency of predation between early- and late-season nests (Table 20). However, variation in predation rates among shellpiles was found in the early season primarily because 62% of early-season nests at North Conjers were predated (Table 20). The relationship between predation and nearest-neighbor distance showed that only for Common Terns at Wire Narrows West were denser nests more immune from predation than were more dispersed nests (Table 21).

Ruddy Turnstones had a substantial impact on nest success in very early-season nests (Table 20). On May 18, 13 Gull-billed Tern nests were found on Wire Narrows East, five in an area visible from the observation platform. On May 19, a Ruddy Turnstone was observed predating nests on Wire Narrows East. Only two Gull-billed Terns were observed incubating on the morning of May 19. A Ruddy Turnstone was observed walking from one nest to the next, eating the contents. A visit to Wire Narrows East found that nine Gull-billed Tern nests had been predated. In total, Ruddy Turnstones predated 12 of the first 14 Gull-billed Tern nests on Wire Narrows East. Ruddy Turnstones were observed at the colonies from May 9 through June 21. Ruddy Turnstones reappeared in late July when the majority of nests were hatched, but no nests were predated by turnstones in the late season.

Nearest-Neighbor Distance (Question 13)

Nearest-neighbor distance significantly affected hatching success for Common Terns at Wire Narrows West, East, and Man & Boy (Table 22). Black Skimmer hatched nests were closer together than were failed nests, although the results were not significant. Gull-billed Terns had similar nearest-neighbor distances for hatched and failed nests.

Flooding

There was one major episode of flooding beginning on June 7 and continuing through to June 14. During this time period, 47% of all the nests on all shellpiles were flooded. On June 7, the actual tide in Wachapreague Channel (NOAA 2002) was 0.45 m higher than the predicted tide (VIMS 2002, Appendix 14). These high tides may have been caused by a low-pressure system offshore. Although most nests were flooded on

June 7, a few more were lost later in the week. On June 14, the highest high reading was 1.89 meters above mean lowest low water, and the highest reached all summer 2002. This value was the highest reading since 1979 for that date. This flood had major effects on all 5 sites. Wire Narrows West had the largest amount of used habitat flooded (Figure 11, Table 23), while Man & Boy had the smallest area flooded (Table 23). The number of nests in the flooded areas decreased from early to late nests (Table 23) at all shellpiles except Wire Narrows West.

Some nests were also lost to flooding during the late May spring high tides. However, these tides were barely above predicted (0.05 m) and did not reach previous highest high records and were below the average of the previous 20 years. Floods also threatened nests in late July, but these tides did not reach the extent of early June.

Overall Hatching Success (Question 14)

Gull-billed Terns were the only species that had more nests hatch (Figure 5, Figure 12) than fail, all at Wire Narrows West. American Oystercatchers had the lowest nest success, with a conservative estimate of 26% of nests hatching, although the fate of 32% of nests was unknown. When I used a multiple logistic regression to determine which variables (elevation, date of nest-initiation, clutch size or nearest-neighbor distance) were most important in predicting hatching success, the results differed among sites and species (Table 24). Elevation and date of nest-initiation were important in determining hatching success for Common Terns at all sites analyzed (n=3), with higher elevation and later date of nest-initiation improving hatching success.

Table 2. Number of nests of 4 waterbird species in experimentally elevated plots.

Site	Number of nests (% of total) Experimental Plots	Control Plots
Wire Narrows West	19 (6)	10 (3)
Wire Narrows East	4 (2)	5 (3)
Man & Boy	5 (3)	5 (3)
South Conjers	8 (8)	15 (15)
North Conjers	2 (7)	0 (0)

*There were no differences in frequencies of nests in experimental versus control plots at any site based on chi-square analysis.

Table 3. Nest elevation compared to random point elevation for early and late nests for 3 waterbird species. Bold values are significantly lower than random points, italicized values are significantly higher than random points.

Site	n	mean elevation ± 1 SD	P	T*
Wire Narrows West				
Random Points	25	1.08 ± 0.1		
COTE early nests	105	**0.98 ± 0.09**	0.0001	-4.9
COTE late nests	82	**1.01 ± 0.07**	0.005	-3.03
GBTE early nests	17	1.13 ± 0.06	0.124	
GBTE late nests	30	*1.14 ± 0.06*	0.007	2.84
BLSK early nests	48	1.07 ± 0.07	0.7	
BLSK late nests	11	1.06 ± 0.05	0.6	
Wire Narrows East				
Random Points	25	1.13 ± 0.12		
COTE early nests	74	**0.86 ± 0.15**	0.0001	-8.55
COTE late nests	65	**1.08 ± 0.12**	0.06	-1.91
Man & Boy				
Random Points	25	1.04 ± 0.23		
COTE early nests	74	0.99 ± 0.24	0.26	
COTE late nests	79	1.13 ± 0.18	0.12	
South Conjers				
Random Points	25	1.28 ± 0.13		
COTE early nests	37	*1.36 ± 0.14*	0.03	2.21
COTE late nests	55	*1.36 ± 0.15*	0.02	2.35
North Conjers				
Random Points	25	1.33 ± 0.13		
COTE early nests	10	*1.52 ± 0.07*	0.0001	4.4
COTE late nests	13	*1.51 ± 0.04*	0.0001	6.38

*Results of t-test comparing elevation of nests to that of random points, listed only for significant ($P<0.05$) comparisons..

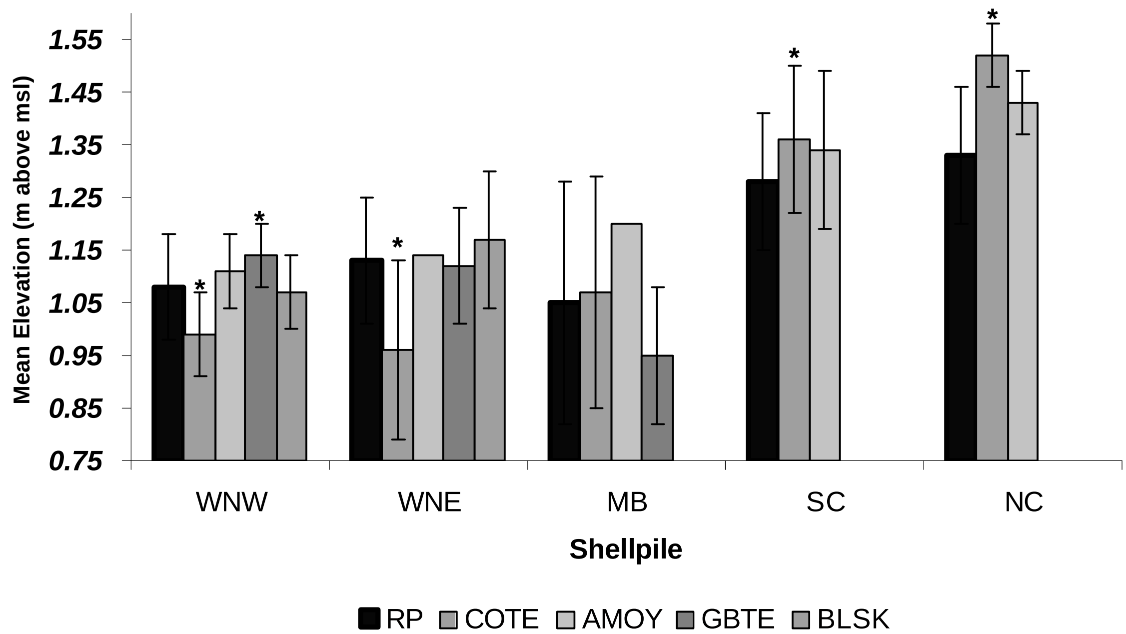


Figure 2. Nest elevation (mean ± 1 SD) vs. random point (RP) elevation at 5 shellpiles for Common Terns (COTE), Gull-billed Terns (GBTE), Black Skimmers (BLSK), and American Oystercatchers (AMOY).Shellpile codes: WNW = Wire Narrows West, WNE = Wire Narrows East, MB = Man & Boy, SC = South Conjers, NC = North Conjers.

*Indicates significant difference from random point elevations: WNW-COTE T=-4.75, P<0.001, COTE nest elevations lower than random points; WNW-GBTE T=2.86, P=.008, nest elevations higher than random points; WNE-COTE T=-4.76, P<0.001, nest elevations lower than random points; SC-COTE T=2.51, P=0.01, nest elevations higher than random points; NC-COTE T=6.53, P<0.001, nest elevations higher than random points.

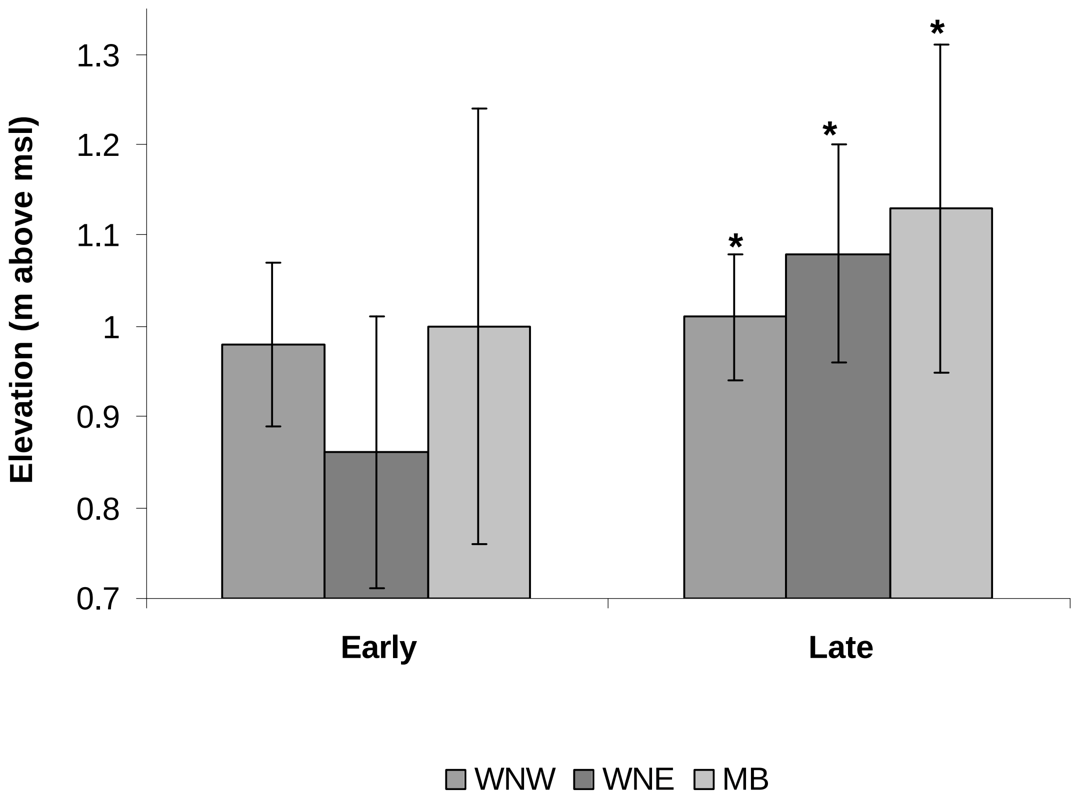


Figure 3. Common Tern nest elevation (mean ± 1 SD) at 3 shellpiles (see Fig. 2 for site codes): early vs. late nests.
 * Significant difference between early nest elevation and late nest elevation. Early nests are significantly lower than late nests. WNW: T=-2.93, P=0.004, n=187 nests; WNE: T=-10.34, P<0.001, n=139 nests; MB: T=10.34, P<0.001, n=153 nests.

Table 4. Nest substrate compared to random points substrate for 3 waterbird species.

Site	Species	n	Substrate % shell-wrack	% shell	% wrack
WNW					
	RP	25	28	64	8
	COTE[a]	181	19	17	65
	GBTE[b]	47	6	94	0
	BLSK[c]	59	7	71	22
WNE					
	RP	25	24	76	0
	COTE[a]	118	24	14	62
	GBTE[d]	18	28	61	11
MB					
	RP	25	24	68	8
	COTE[a]	151	51	23	26
	GBTE[c]	16	75	6	19
SC					
	RP	25	0	96	4
	COTE[a]	92	35	26	39
NC					
	RP	25	16	64	20
	COTE[c]	23	17	0	83

a: P<0.001 for chi-square test on contingency table comparing nest substrate to random points: WNW-COTE ?2=35.26; WNE-COTE ?2=46.55; MB-COTE ?2=20.82, SC-COTE ?2=39.79; all using more wrack and less shell than random points.
b: wrack omitted from analysis; ?2 = 7.3, P=0.007, 25% of cells had <5 but >1 expected values.
c: cells in contingency table had < 5 but >1 expected values; WNW-BLSK ?2=8.1, P=0.02; MB-GBTE ?2=13.8, P=0.001; NC-COTE ?2=21.4, <0.001.
d: sample size too small for analysis (expected values in contingency table had <1 observation)

Table 5. Nest exposure compared to random point exposure for 3 waterbird species.

Site	Species	n	Exposure % exposed	% protected	% neutral
WNW					
	RP	25	20	40	40
	COTE[a]	179	82	0	18
	GBTE[b]	47	4	0	96
	BLSK[a]	59	25	0	75
WNE					
	RP	24	25	54	21
	COTE[a]	139	76	0	24
	GBTE[a]	15	47	0	53
	BLSK[c]	9	11	0	89
MB					
	RP	25	36	44	20
	COTE[a]	151	34	11	55
	GBTE[b]	15	0	53	47
SC					
	RP	25	68	24	8
	COTE[a]	92	60	3	37
NC					
	RP	25	32	56	12
	COTE[a]	23	13	0	87

a: chi-square analysis on contingency table: WNW-COTE P<0.001, ?2=88.18; WNW-BLSK P<0.001, ?2=27.08; WNE-COTE P<0.001, ?2=88.08; WNE-GBTE P=0.002, ?2=12.35; MB-COTE P<0.001, ?2=19.73; SC-COTE P<0.001, ?2=16.56; NC-COTE P<0.001, ?2=28.8. WNW and WNE COTE using exposed sites and at MB, SC, and NC COTE using neutral sites.
b: cells in contingency table had < 5 but >1 expected values; WNW-GBTE ?2=129.6, P<0.001; WNW-MB ?2=7.8, P=0.02.
c: sample size too small for analysis (expected values in contingency table had < 1 observations).

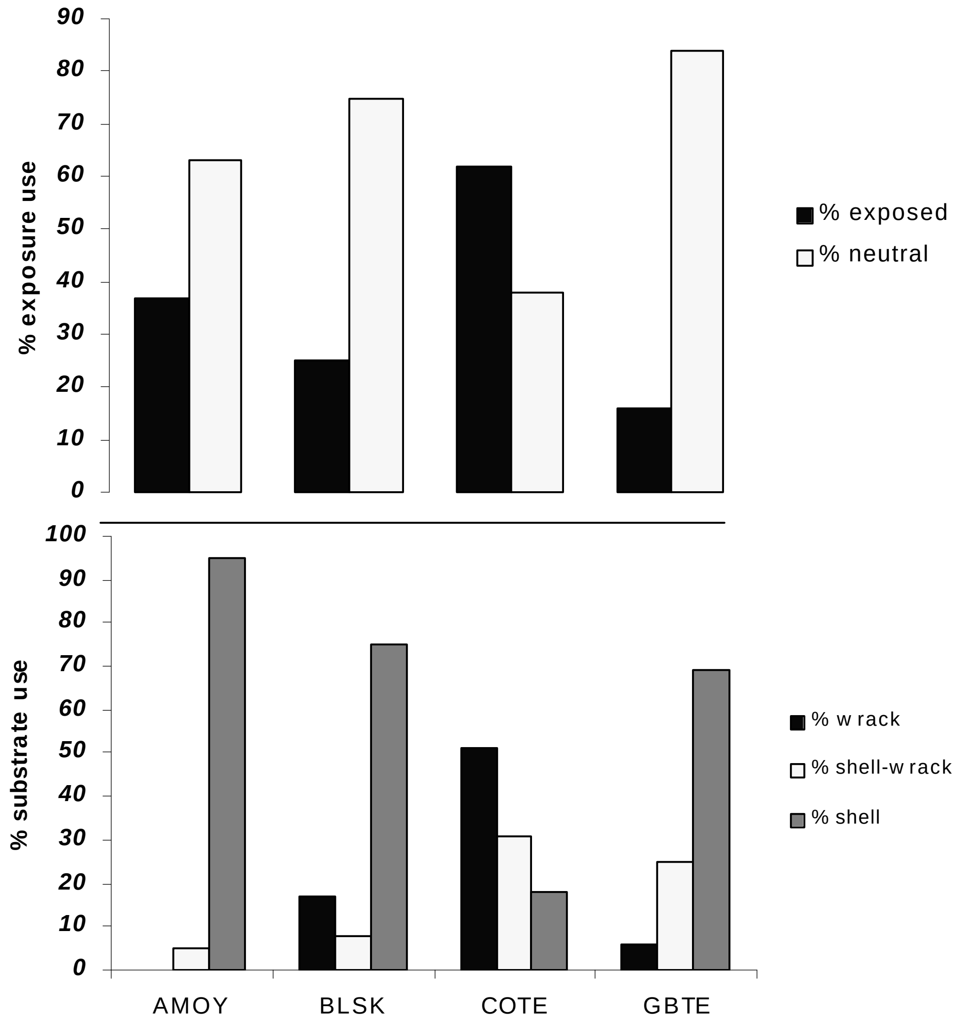


Figure 4. Substrate and exposure use by 4 waterbird species nesting at 5 shellpiles sites, data combined.

Table 6. Comparison of nest elevations at different exposures to open water.

Site	Exposure	n	mean elevation (m) ± 1 S.D.
WNW[a]			
	Exposed	166	0.99 ± .08
	Neutral	125	1.09 ± .08
WNE[a]			
	Exposed	114	0.92 ± .15
	Neutral	49	1.14 ± .13
MB[b]			
	Exposed	52	0.89 ± .15
	Neutral	92	1.2 ± .16
	Protected	26	0.9 ± .14
SC[a]			
	Exposed	58	1.32 ± .13
	Neutral	38	1.42 ± .14
NC			
	Exposed	4	1.42 ± .01
	Neutral	26	1.5 ± .003

T-test or ANOVA comparing elevations of different exposures.
a: WNW T=-11.53, P<0.001; WNE T = -0.16, P<0.001; SC T = 3.57, P<0.001. Neutral sites significantly higher than exposed.
b: MB ANOVA F=84.33, P<0.001, Tukey's studentized range test: exposed sites are significantly lower than protected and neutral sites, protected sites are significantly lower than neutral sites.

Table 7. The elevation of nests on different substrates on each shellpile.

Site	Substrate	n	mean elevation (m) ± 1 S.D.
WNW[a]			
	Shell-Wrack	41	1.03 ± .09
	Shell	121	1.08 ± .08
	Wrack	130	0.99 ± .08
WNE[a]			
	Shell-Wrack	33	1.04 ± .01
	Shell	33	1.18 ± .01
	Wrack	76	0.95 ± .02
MB[a]			
	Shell-Wrack	90	1.08 ± .03
	Shell	38	1.2 ± .05
	Wrack	42	0.87 ± .03
SC			
	Shell-Wrack	32	1.37 ± .03
	Shell	29	1.37 ± .02
	Wrack	36	1.34 ± .02
NC[b]			
	Shell-Wrack	5	1.44 ± .05
	Shell	6	1.43 ± .07
	Wrack	19	1.53 ± .05

ANOVA comparing elevations of the 3 substrates.
a: WNW, F=45.65, P<0.001; WNE, F=40.85, P<0.001; MB, F=32.36, P<0.001; Tukey's studentized range test: all comparisons different at P=0.05.
b: NC F=9.16, P=0.001, Tukey's studentized range test, wrack is significantly different from shell-wrack and from shell.

Table 8. Frequency and elevation of nests near vegetation at 2 shellpiles.

Site	Species	Near Vegetation[a]	n (%)	mean elevation (m) ± 1 S.D.
WNW	COTE[b]	No	91 (47)	1.01 ± .06
		Yes	96 (52)	0.98 ± .09
	GBTE[bc]	No	14 (30)	1.17 ± .05
		Yes	33 (70)	1.12 ± .06
	BLSK[c]	No	36 (63)	1.07 ± .06
		Yes	23 (37)	1.07 ± .08
WNE	COTE[bc]	No	111 (75)	0.98 ± .18
		Yes	28 (25)	0.87 ± .11

a: If nests < 30 cm from vegetation = "yes", if > 30 cm = "no"

b: T-test comparing elevation of nests near vegetation and far from vegetation.WNW-COTE T=1.95, P=0.05; WNW-GBTE T=2.87, P=0.006; WNE-COTE T=40.7, P<0.001.

c: Chi-square analysis on contingency table comparing the number of nests < 30 cm from vegetation to nests > 30 cm from vegetation. WNW-GBTE, ?2=7.68, P=0.005, more nests near vegetation. WNW-BLSK, ?2=4.14, P=0.036, more nests far from vegetation. WNE-COTE, ?2=32.13, P<0.001, more nests far from vegetation.

Table 9. Nearest-neighbor distances for 4 waterbird species.

Site	Species	Nearest-Neighbor Distance (m ± 1 S.D.) (n) Overall	Early	Late
WNW				
	COTE[a]	1.00 ± .65 (179)	1.11 ± .7 (97)	0.88 ± .6 (82)
	GBTE[a]	0.78 ± .37 (47)	1.04 ± .47 (17)	0.63 ± .18 (30)
	BLSK	0.92 ± .92 (59)	0.96 ± .86 (48)	0.76 ± .34 (11)
	AMOY	30.62 ± 24.1 (5)		
WNE				
	COTE	1.17 ± .84 (105)	1.28 ± 1.03 (51)	1.03 ± .55 (34)
	GBTE	1.25 ± .67 (16)		
	BLSK	0.92 ± .27 (7)		
	AMOY[b]			
MB				
	COTE	1.57 ± 1.55 (150)	1.56 ± 1.24 (72)	1.58 ± 1.8 (78)
	GBTE	0.88 ± .54 (16)		
	AMOY[b]			
SC				
	COTE	1.19 ± .92 (89)	1.36 ± 1.14 (34)	1.11 ± .76 (55)
	AMOY	7.83 ± 4.3 (5)		
NC[c]				
	AMOY	21.12 ± 11.83 (7)		

a: late nests significantly closer than early nests; WNW-COTE: T = 2.34, P=0.02; WNW-GBTE: T = 3.4, P=0.003.

b: no other nests on shellpile when AMOY nest was initiated.

c: nearest-neighbor distances not calculated for NC-COTE.

Table 10. Area and nest density of 5 shellpiles.

	Area of used habitat (m^2)	**Area of available habitat (m^2)**	**% of available habitat used**	**Density ($nests/m^2$) in used habitat**	**Density ($nests/m^2$) in available habitat**
WNW	341.03	886.73	38	0.93	0.36
WNE	171.97	543.75	32	1.03	0.33
MB	304.44	661.21	46	0.56	0.26
SC	104.94	108.13	97	1.02	0.92
NC	48.96	521.65	10	0.61	0.06

Table 11. Density of nests by species for each shellpile. Density is $nests/m^2$.

		Density in used area	**Early nest density in used**	**Late nest density in used**	**Density on available habitat**
COTE					
	WNW	0.57	0.74	0.51	0.22
	WNE	0.87	0.67	1.22	0.33
	MB	0.56	0.48	0.34	0.26
	SC	0.9	0.46	0.68	0.88
	NC	0.47	0.24	0.32	0.04
GBTE					
	WNW	0.83	0.46	0.74	0.05
	WNE	0.72			0.03
	MB	1.92			0.02
BLSK					
	WNW	0.5	0.62	0.27	0.07
	WNE	1.24			0.02

Table 12. Frequency of interspecific aggressive interactions and outcomes among 4 species at Wire Narrows, Chincoteague.

No. of times initiates aggression at (no. times initiator "won" interaction): Initiator species

Recipient	AMOY	COTE	GBTE	BLSK
AMOY	-	0	0	0
COTE	0	-	3 (1)	2 (1)
GBTE	0	3 (2)	-	4 (2)
BLSK	6[a] (6)	7 (4)	20[b] (15)	-

note: the number of "won" interactions may not add to the number of initiated interactions because some interactions ended in a stand-off.

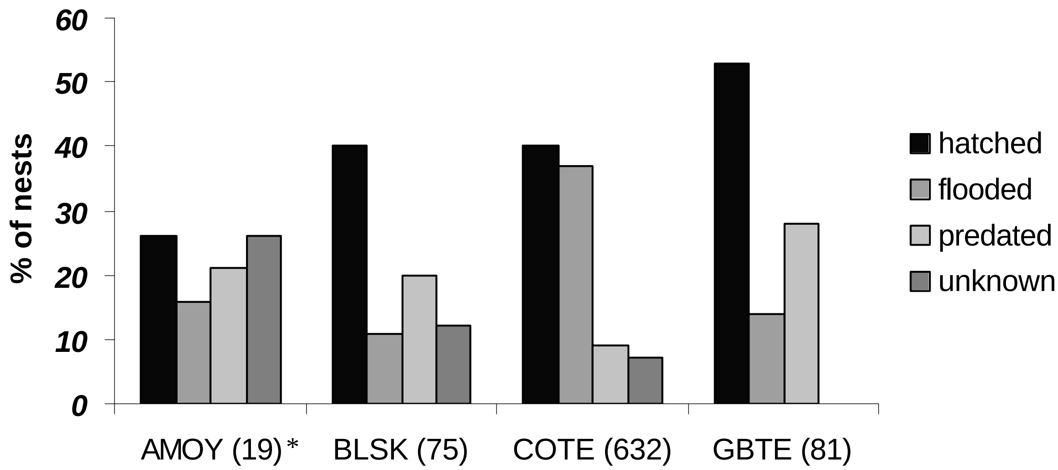
a: all same AMOY chasing BLSK on same day
b: 17 from same GBTE pair on an experimental plot WNW to a BLSK pair

Table 13. The effect of elevation on hatching success for 3 species of waterbirds.

Site	Species	Mean Elevation (m ± 1 S.D.) (n) Hatched	Mean Elevation (m ± 1 S.D.) (n) Failed	
WNW				
	COTE	1.02 ± .07 (83)	0.97 ± .08 (90)	**
	GBTE	1.13 ± .06 (39)	1.18 ± .07 (8)	*
	BLSK	1.07 ± .07 (26)	1.06 ± .06 (28)	ns
WNE				
	COTE	1.08 ± .11 (57)	0.9 ± .16 (52)	**
MB				
	COTE	1.14 ± .18 (72)	0.97 ± .25 (69)	**
SC				
	COTE	1.41 ± .12 (34)	1.32 ± .15 (54)	**
NC				
	COTE	1.52 ± .07 (9)	1.5 ± .05 (12)	ns

Analyzed with a logisitc regression looking at the effects of elevation on hatching success.
* WNW-GBTE ?2=4.7, P=0.03. Decreased hatching success with increasing nest elevation.
** WNW-COTE: ?2=19.1, P<0.001; WNE-COTE ?2=27.1, P<0.001; MB-COTE ?2=15.8, P<0.001; SC-COTE ?2=7.19, P<0.001. All show increased hatching success with increasing nest elevation.

Figure 5. Nest outcomes combined for all shellpiles.
(number of nests)



* Fate of 6 of 19 AMOY nests unknown.

Table 14. Relationship between elevation and hatching success in 3 waterbird species: early and late nests.

		Early			Late		
Site	**Species**	**Mean Elevation (m ± 1 S.D.) (n) Hatched**	**Mean Elevation (m ± 1 S.D.) (n) Failed**		**Mean Elevation (m ± 1 S.D.) (n) Hatched**	**Mean Elevation (m ± 1 S.D.) (n) Failed**	
WNW							
	COTE	1.04 ± .06 (27)	0.95 ± .09 (74)	*	1.02 ± .07 (56)	1.0 ± .06 (16)	ns
	GBTE	1.13 ± .06 (14)	1.16 ± .09 (3)	ns	1.13 ± .06 (25)	1.2 ± .07 (5)	**
	BLSK	1.07 ± .08 (22)	1.07 ± .06 (22)	ns	1.07 ± .05 (4)	1.06 ± .05 (6)	ns
WNE							
	COTE	1.14 ± .11 (7)	0.85 ± .12 (44)	*	1.08 ± .11 (50)	1.14 ± .11 (8)	ns
MB							
	COTE	1.19 ± .17 (25)	0.89 ± .21 (44)	*	1.11 ± .17 (47)	1.18 ± .21 (19)	ns
SC							
	COTE	1.43 ± .2 (5)	1.34 ± .13 (30)	ns	1.41 ± .11 (29)	1.3 ± .16 (24)	***

Analyzed with a logisitc regression looking at the effects of elevation on hatching success for early and late nests, separately.

* P<.001: WNW-COTE early ?2 = 14.25, WNE-COTE early ?2=11.26, MB-COTE early ?2=17.28.

**WNW-GBTE late, ?2=4.34, P=0.04.

***SC-COTE late ?2 = 6.24, P=0.01.

ns: not significant

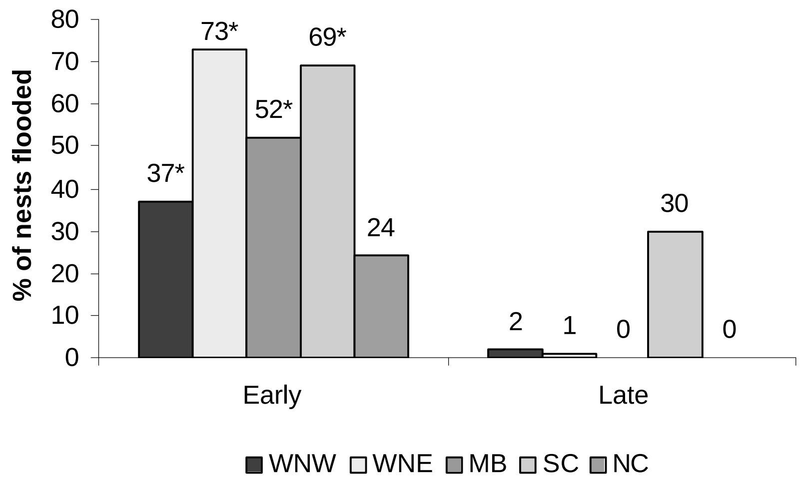


Figure 6. Flooding in early and late nesting seasons at 5 sites.
*Results from chi-square analysis on contingency table. WNW ?2=52.15, P<0.001, n=309; WNE ?2=89.77, P<0.001, n=177; MB ?2=52.96, P<0.001, n=178; SC ?2=14.96, P<0.001, n=99. There was no significant difference for NC.

Table 15. Relationship between nest substrate and hatching success for 3 species of waterbirds. Bold shows substrate with highest hatching success.

Site	Species	n	% hatch on shell-wrack	% hatch on shell	% hatch on wrack
WNW					
	COTE	181	**54**	45	44
	GBTE	47	67	**84**	N/A
	BLSK	58	20	49	**50**
WNE					
	COTE[a]	140	**68**	53	29
MB					
	COTE[a]	152	**56**	47	26
	GBTE[b]	16	8	**100**	0
SC					
	COTE	90	36	**57**	28
NC					
	COTE	21	25	N/A	**47**

a: Chi-square analysis on contingency table comparing hatching success between substrates.WNE-COTE ?2=15.66, P<0.001; MB-COTE: ?2=8.48, P=0.01. Common Terns have significantly lower hatching success on wrack.
b: sample size not large enough for analysis.

Table 16. Relationship between nest exposure and hatching success in 3 waterbird species.

Site	Species	n	% hatch in exposed	% hatch in neutral	% hatch in protected
WNW					
	COTE	179	44	58	-
	GBTE[a]	47	0	87	-
	BLSK	58	50	45	-
WNE					
	COTE[b]	140	32	63	-
MB					
	COTE[b]	152	25	69	28
	GBTE	16	0	14	17
SC					
	COTE	87	35	43	-
NC					
	COTE	23	33	44	-

a: Chi-square analysis on contingency table ?2=10.18, Fisher's Exact Test P=0.03.
b: Chi-square analysis on contingency table WNE-COTE ?2=10.88, P=0.001; MB-COTE: ?2=28.89, P<0.001.

Table 17. Influence of vegetation on hatching success for Common Terns and Gull-billed Terns.

Site	Species	n	% hatch near vegetation	% hatch with no vegetation
WNW				
	COTE	184	34	59
	GBTE	47	94	57
WNE				
	COTE	105	5	56

Common Terns have lower hatching success near vegetation while Gull-billed Tern hatching success is higher near vegetation. Chi-square analysis on contingency table WNW-COTE ?2=10.8, P=0.001; WNW-GBTE ?2=10.18, P=0.002; WNE-COTE ?2=32.13, P<0.001.

Table 18. Relationship between hatching success and season for 3 waterbird species.

Site	Species	n	Early % hatched	Late % hatched	
WNW					
	COTE	189	23	77	*
	GBTE	47	82	83	ns
	BLSK	58	48	40	ns
WNE[a]					
	COTE	150	9	85	*
MB[b]					
	COTE	152	29	71	*
SC					
	COTE	92	14	55	*
NC					
	COTE	21	30	55	

* Chi-square contingency analysis, WNW-COTE: ?2=52.3, P<0.001; WNE-COTE: ?2=81.9, P<0.001; MB-COTE: ?2=26.6, P<0.001; SC-COTE: ?2=15.8, P=0.001. Hatching success significantly higher in late season nests.
a: only two late GBTE nests, and 2 early BLSK nests.
b: only two late GBTE nests

Figure 7. Common Tern Nest Initiation Dates

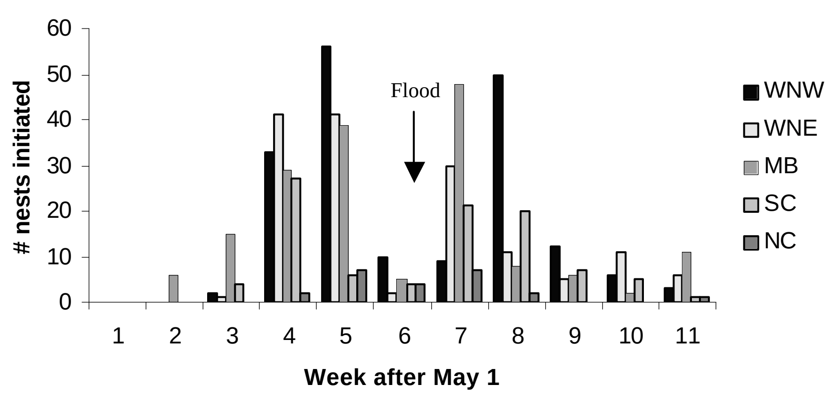


Figure 8. Gull-billed Tern Nest Initiation Dates

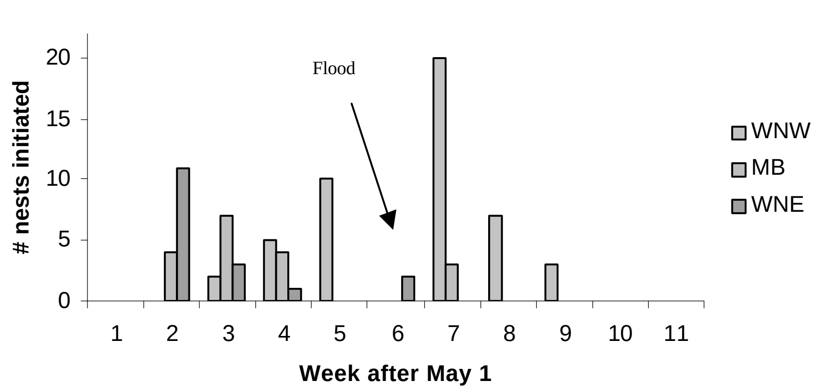


Figure 9. Black Skimmer Nest Initiation Dates

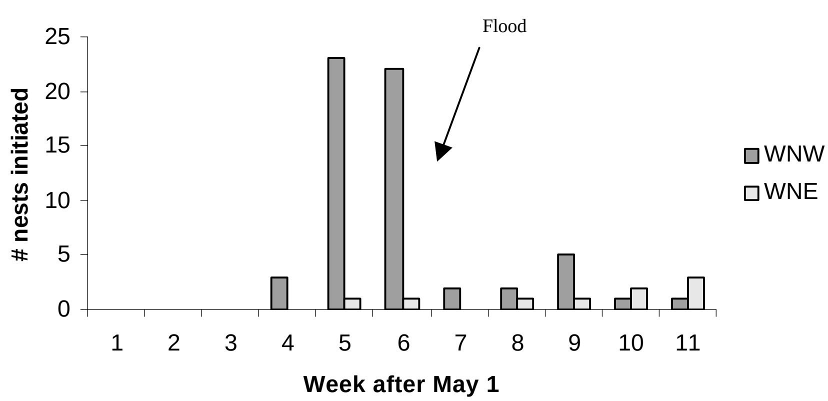


Table 19. Clutch size (mean ± 1 S.D.) and season effects for 3 species of waterbirds.

Site	Species	n	Early Nests	Late Nests	
WNW					
	COTE	174	2.01 ± .66	2.1 ± .53	ns
	GBTE	47	2.24 ± .75	2.47 ± .51	ns
	BLSK	56	3.21 ± .99	2.11 ± .78	*
WNE					
	COTE	144	2.28 ± .58	2.06 ± .62	*
MB					
	COTE	143	2.07 ± .59	1.85 ± .51	*
SC					
	COTE	76	2.44 ± .58	1.78 ± .61	*
NC					
	COTE	20	1.86 ± .69	2.15 ± .5	ns

* T-test comparing clutch sizes of early and late nests: WNW-BLSK T=3.12, P=0.003; WNE-COTE T=2.21, P=0.03; MB-COTE T=2.4, P=0.02; SC-COTE T=4.46, P<0.001.

Table 20. Predation rates on all waterbird species among 5 shellpiles.

	% nests predated (n)				
	All Predation			Ruddy Turnstone predation	
Site	Total	Early*	Late	Total	Early
WNW	13 (39)	15 (26)	11 (13)	7 (2)	4
WNE	13 (22)	15 (15)	11 (7)	13 (8)	13
MB	17 (29)	18 (19)	15 (10)	11 (6)	10
SC	3 (3)	3 (1)	3 (2)	1 (1)	2
NC	37 (10)	62 (10)	15 (2)	7 (2)	41
Total	13 (103)	16 (71)	9 (32)	39 (5)	10

* there were no statistically significant differences using chi-square analysis between frequency of predation of early versus late nests.

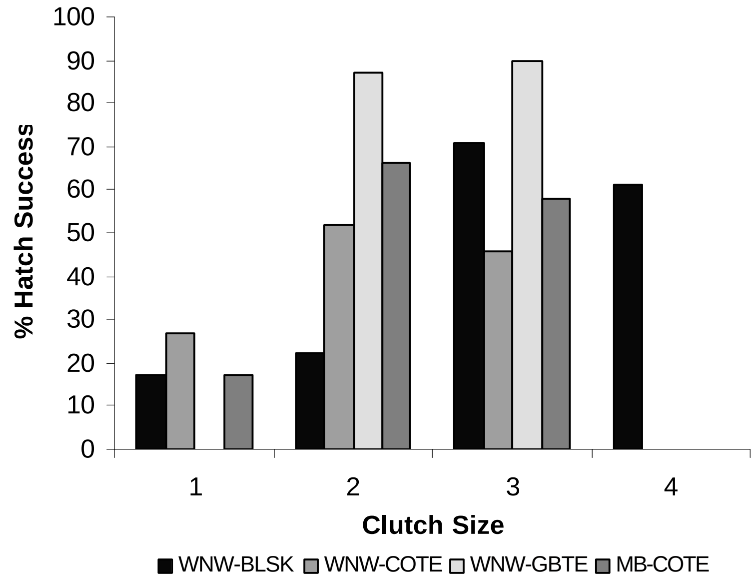


Figure 10. Hatching success versus clutch size in 5 species of waterbirds. Results of logistic regression analyzing effects of clutch size on hatching success. WNW-BLSK: ?2=9.76, P=0.02, n=52; WNW-COTE: ?2=4, P=0.045, n=167; WNW-GBTE: ?2=5.26, P=0.02, n=47; MB-COTE: ?2=8.33, P=0.004, n=130. Hatching success increases with larger clutch sizes.

Table 21. Nearest-neighbor distances for predated and not-predated nests.

Site	Species	Mean (± 1 S.D.) Nearest-Neighbor Distance (in m) Predated	Not Predated	
WNW				
	COTE	1.65 ± .91 (15)	0.96 ± .61 (141)	**
	GBTE	0.83 ± .37 (6)	0.77 ± .39 (39)	ns
	BLSK	0.83 ± .31 (13)	0.97 ± .92 (38)	ns
WNE				
	COTE	1.74 ±1.24 (8)	1.15 ± .82 (96)	ns
MB				
	COTE	1.31 ± 1.1 (21)	1.54 ±1.6 (112)	ns

T-test comparing mean nearest-neighbor distance between predated and not-predated nests only significant for WNW-COTE T=3.94, P<0.001.

Table 22. Nearest-neighbor distance and hatching success for 3 waterbird species, n in parentheses

Site	Species	Distance to nearest neighbor (m ± 1 S.D.) Hatched	Failed	
WNW				
	COTE	0.86 ± .42 (83)	1.19 ± .83 (82)	**
	GBTE	0.78 ± .38 (39)	0.75 ± .35 (8)	ns
	BLSK	0.78 ± .37 (26)	1.03 ± 1.04 (28)	ns
WNE				
	COTE	0.97 ± .66 (53)	1.47 ± 1.04 (50)	**
MB				
	COTE	1.66 ± 1.83 (72)	1.31 ± 1.06 (63)	ns
SC				
	COTE	1.03 ± .55 (34)	1.28 ± 1.03 (51)	ns

**Results from logistic regression analyzing effects of nearest-neighbor distance on hatching success: WNW-COTE ?2 = 9.04, P=0.003; WNE-COTE ?2 =6.7, P=0.01.

Figure 11. Distribution of nests on Wire Narrows West in relation to flooding.

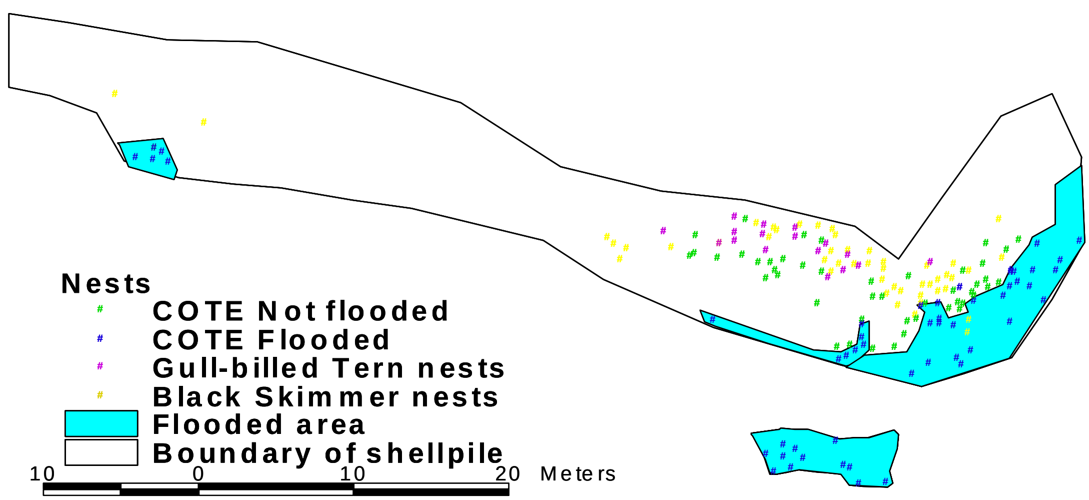


Table 23. Area of habitat used by nesting waterbirds flooded June 7-14, 2002 at 5 shellpile sites and percentage of nests in the flooded area.

Site	Area flooded (m^2)	% used habitat flooded	% of nests in flooded area Early	% of nests in flooded area Late
WNW	142	42	57	58
WNE	66	38	85	11
MB	66	22	52	32
SC	30	29	71	53
NC	16	32	30	8

Table 24. Multiple logistic regressions using elevation, nest-initiation date, clutch size, and nearest-neighbor distance to explain hatching success.

			n	Wald ?2	P
Wire Narrows West					
	COTE		156		
		intercept		26.4	<0.001
		elevation		15.7	<0.001
		nest-initiation date		20	<0.001
		clutch		6.7	0.001
	GBTE		47		
		intercept		3.6	0.06
		elevation		4.1	0.04
		clutch		4.6	0.03
	BLSK[a]		48		
Wire Narrows East					
	COTE		105		
		intercept		21.3	<0.001
		elevation		15.1	<0.001
		nest-initiation date		14.8	<0.001
		nearest-neighbor		5.9	0.02
Man & Boy					
	COTE		116		
		intercept		21.6	<0.001
		elevation		10.1	0.02
		nest-initiation date		12.5	<0.001
		clutch		13.8	<0.001
		nearest-neighbor		4.2	0.04

a: no effects met the 0.05 significance level for entry into model.

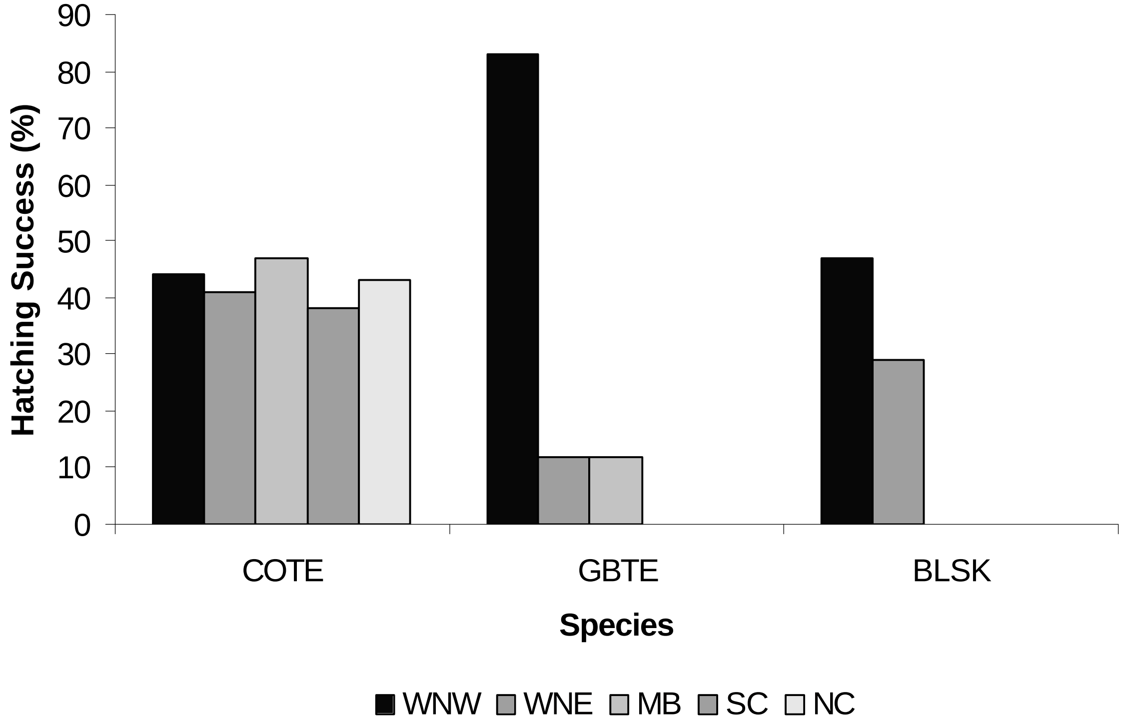


Figure 12. Hatching success of Common Terns, Gull-billed Terns, and Black Skimmers at each shellpile.

Discussion

Nest-Site Selection

Physical Factors

Experimentally elevated plots were not preferentially selected for at any of the shellpiles, or by any species, despite the extra protection from floods elevated plots provided to nesting birds. A number of other factors involved in nest-site selection could explain this including substrate, vegetation and previous experience at nesting sites. Common Tern nests were only significantly higher than random points at North and South Conjers, which account for only 20% of all Common Tern nests on the shellpiles. Eighty percent of Common Tern nests, therefore, were either of similar elevation to random points or lower. Because Common Terns did not select nest sites based on high elevation locations, elevated plots were not selected for preferentially. In addition, the combination of choosing to nest on wrack and near vegetation may have contributed to the small number of Common Tern nests on elevated plots at both Wire Narrows shellpiles. Gull-billed Tern nests at Wire Narrows West were higher than randomly available, and were concentrated around one of the pairs of experimental plots. At Wire Narrows East and Man & Boy, Gull-billed Tern nests were not different in elevation from random points. Gull-billed Terns may have been primarily selecting sites based on previous nesting experience at these shellpiles. For example, nests at Man & Boy were at the same place as nests had been found in 2001, on a low section of one ridge.

Nine percent of Black Skimmer nests were in elevated plots. Black Skimmers chose to nest on shell preferentially, and their nest elevation was not different from what was available. Black Skimmers choose to nest among Gull-billed Terns and Common

Terns (Erwin 1977b, Pius and Leberg 1997), and the location of earlier tern nests may have influenced their nest-site selection. American Oystercatcher nests were higher than random points at all sites, and two nests (11%) were in elevated plots.

Although elevation may not be the most critical factor in initial nest-site choice, it may become more important later in the season. At Wire Narrows and Man & Boy, late nests of Common Terns were significantly higher than early nests, and late nests at Man & Boy were significantly higher than random points. The flooding on June 7 may have caused birds to renest at higher elevations, especially because for most of the week after June 7 areas of the shellpiles that Common Terns had previously nested on were underwater.

With respect to substrate, Common Terns at all shellpiles used wrack at a higher frequency than that randomly available on the shellpile. Burger and Lesser (1978) pointed out that wrack provides good camouflage for the dark brown Common Tern eggs. This is especially true compared to the white of bleached oyster shells. Burger and Lesser (1978) found that over 80% of Common Tern in New Jersey on salt-marsh islands nested on wrack. Eighty-two percent of Common Terns in this study used either wrack or shell and wrack as nest substrates. The Common Terns nested on wrack that had been deposited during earlier winter and spring storms, and also on wrack that was deposited during the June 7 flood. At Wire Narrows East, Man & Boy, and South Conjers, the percentage of nests on wrack decreased during the season. This change may be a result of birds moving to higher or different areas than what was flooded in the early season, since wrack nests had the lowest elevations at those sites. However, wrack nests were also lower at Wire Narrows West yet Common Terns selected wrack at the same frequency in early and late nests. Many late Common Tern nests at Wire Narrows West were on the wrack line deposited by the June 7 flood and this may account for the difference.

The choice of shell as a nest-site substrate for Gull-billed Terns (69%) and Black Skimmers (75%) suggest that their lighter-colored eggs (relative to Common Terns) may be better camouflaged on shellpiles. Leberg et al. (1995) also found that Gull-billed Terns disproportionately selected shell for nesting, but felt that Black Skimmer nest choice was more influenced by the presence of nesting Gull-billed Terns than the actual substrate. Shell nests had the highest elevations at all the shellpiles used by Gull-billed Terns and Black Skimmers and this also may have contributed to their preference of shell as a substrate. American Oystercatchers, another species with light, creamy colored eggs, used shell for 95% of nests, which is typical of other locations for this species (Nol and Humphrey 1994).

Exposed sites were more attractive to Common Terns than randomly available sites at Wire Narrows and South Conjers. At Man & Boy and North Conjers Common Terns chose neutral sites preferentially. Overall, 62% of Common Tern nests were at exposed sites. At Wire Narrows the exposed sites were primarily low-lying areas, near the tide line, with sparse vegetation. Common Terns may have been attracted to these areas because these are the areas where wrack had been deposited and because of the presence of vegetation for protection and cover. At Man & Boy and North Conjers there is little vegetation cover, and at North Conjers there was a lot of wrack on neutral sites. At all shellpiles exposed sites had lower elevations than neutral sites. Similarly, Burger and Lesser (1978) found that most Common Tern colonies on marsh islands were on the side of the island exposed to open water. Gull-billed Terns, Black Skimmers, and

American Oystercatchers all preferred neutral sites, and generally avoided the low-lying vegetated areas that Common Terns preferred.

Vegetation also may have influenced nest-site selection. Common Terns, Gull-billed Terns, and Black Skimmers will nest near vegetation if present and Gull-billed Terns particularly seemed to select sites near vegetation, if the vegetation was on higher areas of the shellpile. Kotliar and Burger (1986) reported Common Terns nesting near short, sparse vegetation that is similar to what was available on the shellpiles. Erwin (1979) found that Common Terns nested near vegetation, with Black Skimmers in more open areas among the terns, while Gochfeld (1978) found that Black Skimmers had less cover at their nests than Common Terns. At Wire Narrows West, the areas with vegetation that Gull-billed Terns and Black Skimmers used were much more open, with one or two plants every few meters. The areas with vegetation used by Common Terns tended to have a denser distribution of plants, though most were still very short with open space in between plants. The presence of vegetation near a nest to provide cover and protection appears to be an important factor in nest-site selection. Areas of Wire Narrows West with dense vegetation were devoid of nests, but chicks were seen hiding for cover in these areas. Only two American Oystercatcher nests, both at Wire Narrows West, were near vegetation. In addition, vegetation may have influenced use of experimental plots. The elevated plot on Wire Narrows West with a high density of nests had a plant growing in the middle of the plot. Many Gull-billed Tern nests were around this plant (and similarly around another plant at Wire Narrows East) and this may have contributed to their use of this plot for nests.

Biological and Social Factors

Common Tern nearest-neighbor distances are similar to those reported elsewhere (Erwin 1977a, Burger and Lesser 1978), although on the lower end. Burger and Lesser (1978) suggested that nearest-neighbor distance varied as a function of habitat area. This would explain why nearest-neighbor distances are low on the shellpiles since the area used by nesting birds at the shellpiles was limited. Gull-billed Terns nearest-neighbor distances are much closer than reported elsewhere (Sears 1978, Moller 1981). However, distances between conspecifics were farther (1.15 m to 3.4 m). Black Skimmer nearest-neighbor distances were on the lower end of what is reported elsewhere (Gochfeld and Burger 1994, Pius and Leberg 1997). American Oystercatcher nests were very close together for a solitary species at South Conjers (7.83 m, n=5) although distances at the other shellpiles were greater than 20 m. The highest American Oystercatcher nest density Lauro et al. (1992) found in New York and Virginia was 1.3 and 0.1 nests/km^2, respectively. American Oystercatcher nest density on South Conjers was 48 nests/km^2. Lauro et al. (1992) found that at the highest nest densities in New York, American Oystercatchers were breeding communally, possibly because of a shortage of high quality territory. There was no evidence of communal nesting at any shellpiles despite the high density of American Oystercatcher nests at South Conjers, North Conjers, and Wire Narrows West. Nearest-neighbor distances changed significantly between early and late nests for Common Terns and Gull-billed Terns at Wire Narrows West, with later nests being closer together. Burger and Lesser (1979) also found that birds renesting after a storm nested closer together, probably because of a decrease in suitable habitat.

At Wire Narrows West, Gull-billed Terns nested the closest to other nests. If nearest neighbor distance serves as a proxy for territory size (Burger and Gochfeld 1990) then Gull-billed Terns had the smallest territories, while Common Terns had the largest. In contrast to this study, Erwin (1977a) found that Black Skimmers were more widely dispersed than Common Terns. Black Skimmers nested in close proximity to both Common Terns and Gull-billed Terns at Wire Narrows West in the only area of bare shell used by nesting birds. Because Black Skimmers chose to nest near Gull-billed Terns and Common Terns, possibly to improve nest defense (Erwin 1977b, Pius and Leberg 1997), and also preferred open sites on shell, their nest density might have been higher than expected because of the small area of the used area of the shellpile that suited their preferences.

The highest nesting densities were reached at Man & Boy with 1.92 nests/m^2 for Gull-billed Tern nests. These nests were in a small patch of the shellpile that was also used by Gull-billed Terns in 2001; previous nesting experience at the shellpile may explain the high density of nests in this area.

Aggressive interactions between species did not play a significant role in nest-site selection, at least at the Wire Narrows sites I observed. The locations on the shellpiles where aggressive interactions were observed eventually had high numbers of nesting birds of all species. It is unlikely that the small number of nests on elevated plots was due to the aggressive defense of a nest territory by early-nesting birds.

In addition to the factors mentioned above, the locations of American Oystercatcher nests seemed to play a role in nest-site selection for Common and Gull-billed Terns. American Oystercatcher nests were established in April on all five shellpiles, in some cases probably before the terns and skimmers had arrived. Subsequently, many early Common Tern and Gull-billed Tern nests were located around the early Oystercatcher nests, or in some cases, in the Oystercatcher scrape. In many cases these nest locations became centers of the future colony. For example, at Wire Narrows West there were three American Oystercatcher nests in May when the terns arrived. These three nest locations became the center of the three major nesting areas of the colony. Early nests of terns were established near or in American Oystercatcher nests, and these areas continued to be used throughout the breeding season. This pattern is probably a combination of social attraction influencing nest-site selection, along with previous nesting experience at the shellpiles.

At Wire Narrows West and East, and Man & Boy, in addition to the unused elevated plots, extensive areas of shell at high elevations and closer to the marsh (and so protected from flooding) were not used by any nesting birds. At Wire Narrows some of these areas, because of their proximity to the marsh, were also close to nesting Laughing Gulls. The Laughing Gulls, during the pre-egg laying stage, often stood and defended the area of the shellpile adjacent to their nests. Since Laughing Gulls are known predators of tern and skimmer nests, the birds may avoid nesting on these areas of the shellpiles. The only two late Gull-billed Tern nests at Wire Narrows East were located in a high, protected area of the shellpile near Laughing Gull nests, and were predated. However, I was unable to determine the cause of the predation. However, no Laughing Gulls nested near the colonies at Man & Boy and yet many protected areas of the shellpile were not used.

Nest-Site Selection Summary

Contrary to expected, Common Terns did not choose higher nest-sites than were randomly available on shellpiles. While Common Terns did nest in high locations, the majority of their nests put them at significant risk of flooding. Over 85% of Common Terns nested with 2 m of their nearest-neighbor, indicating that location of other nesting birds is a strong selective force. This can also be seen by the congregation of early nests in areas with an American Oystercatcher nest. The role of previous experience of use of the shellpiles cannot be assessed since accurate locations of Common Tern nests in 2001 or earlier are unknown.

Gull-billed Terns at Wire Narrows West nested in an area protected from flooding and at higher elevations. At Wire Narrows East most nests were predated before the June 7 flood; however, if those nests had been active some would have flooded. At Man & Boy Gull-billed Terns nested on a low-lying area of the shellpile that was completely flooded on June 7. This area was also used by nesting Gull-billed Terns in 2001 and it is possible that this part of the shellpile used to have a higher ridge and more protection from flooding. Since the shellpiles are frequently changed in shape by winter storms, Gull-billed Terns may initially have selected this part of the shellpile when it was higher and now continue to use the same site. At all sites, Gull-billed Terns primarily selected nest sites on shell and on neutral slopes, and in close proximity to other nests.

Black Skimmers at Wire Narrows West 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 chose colony sites based on locations of Gull-billed and Common Tern colony sites (Erwin

1977b, Pius and Leberg 1997), their nest-site selection was probably strongly influenced by social stimulus of nesting near already established tern nests at the shellpiles.

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

Marsh islands provide marginal habitat for nesting terns, skimmers, and oystercatchers because of their low elevations. Providing elevated sites for nests met with very limited success. The elevated plots did not provide the habitat preferred by Common Terns, and may not have been located in areas previously used by Gull-billed Terns, especially at Man & Boy where an elevated plot in the Gull-billed Tern nesting area probably would have protected the nests from flooding. 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. Colony and site-specific factors appear to be important when examining nest-site selection.

Hatching Success

Physical Factors

For all species at all shellpiles, the elevation of a nest influenced its hatching success. Flooding of nests on marsh islands is generally higher than on barrier island beaches (Burger and Gochfeld 1991), however the marsh islands are protected from ground predators. Buckley and Buckley (1980) suggest that Common Tern's ability to adapt to salt marsh nesting may be related to their ability to relay 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 June 7 floods.

Common Tern nests with higher elevations had higher hatching success at all shellpiles except North Conjers. The June 7 floods had a significant effect on these results. At Wire Narrows and Man & Boy early nests had improved hatching success at higher elevations. Black Skimmers hatching success was not affected by elevation and Black Skimmers also had the lowest rates of flooding (Figure 5) of all species, since they primarily nested in an area protected from floods. The hatching success of Common Terns at South Conjers was not affected by elevation in the early season, but only in the late, a reverse trend than the other shellpiles. Thirty percent of late nests at South Conjers flooded, a much higher rate than any other shellpile (Figure 11), and this may have affected the result. It is possible that because of the small size of the shellpile, birds were forced to renest in low-lying areas that flooded early because of competition for limited nesting sites.

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. Nisbet (1977) found that younger Common Terns nested later, and that younger birds had nests with lower elevations (Nisbet et al. 1984). In addition, late nests also often have lower reproductive success than early nests (Spendelow 1982, Nisbet et al.1984, Burger and Gochfeld 1990). In this study, however, late Common Tern nests were higher than early nests and no major floods occurred during the late season, therefore hatching success improved.

Substrate seemed to affect hatching success. Hatching success at Man & Boy, Wire Narrows East and South Conjers was lowest for nests on wrack. Since elevations of wrack nests were lower than that of other substrates, the increased chance of flooding for a wrack nest probably made hatching success lower. At Wire Narrows West and North Conjers, areas with wrack occurred on high grounds and were protected from flooding, therefore hatching success was not different between the different substrates. Nests that were exposed to open water had significantly lower hatching success than exposed sites because of their lower elevations and their proximity to tidal fluctuations.

Vegetation proximity negatively affected Common Tern hatching success, however vegetation and elevation co-vary. Since vegetated areas of a shellpile are lower, these nests were exposed to flooding at a higher frequency than nests on bare shell. While nest-sites near vegetation may have been selected to provide cover for eggs and chicks, their proximity to open water caused higher nest failure. At South Conjers, all but 1 of the 12 nests near vegetation flooded. However, Gull-billed Terns at Wire Narrows West nested near small plants that had grown up through the shell, and these nests were significantly more successful than other nests. For Gull-billed Terns, therefore, the vegetation may have provided protection and cover, while not exposing the birds to floods.

For the physical factors involved in hatching success, it appears that elevation had the strongest effect. As long as nests were low and exposed to flood tides, the substrate used or the presence of vegetation has little effect on hatching success. However, if the elevation of a nest is high enough to protect it from flooding, other factors become more important in explaining hatching success.

Biological and Social Factors

The effect of clutch size, which may reflect parental age or experience (Nisbet et al. 1984), on hatching success was not consistent across shellpiles or species. Clutch size for Common Terns was larger for hatched nests at all shellpiles except South Conjers, but only significantly so at Wire Narrows West and Man & Boy. Other factors not analyzed in this paper, such as age of birds or food availability (Nisbet 1977), may have contributed to this result. Gull-billed Terns at Wire Narrows West had significantly higher hatching success with larger clutch sizes. Clutch sizes for all species were similar to those reported elsewhere (Sears 1978, Erwin 1977b, Nol et al. 1984). At all shellpiles, Common Terns with 2-egg clutches had the highest hatching success. This indicates that the investment of energy required to produce two eggs may be optimal for Common Terns on the shellpiles, or that older, more experienced birds lay 2-egg clutches.

Predation was, overall, not a major cause of nest failure at any of the shellpiles except North Conjers where 64% of early nests were predated. North Conjers had the smallest nesting colony, with a peak of only 13 nests on June 25 in contrast to Wire Narrows West that had a peak over 150 nests. Ruddy Turnstones predated 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 predation rates, probably because fewer birds were present to mob predators. However, South Conjers, which was the second smallest colony but the densest, had the lowest predation rates. Because nests were so dense over the whole shellpile, mobbing of predators was possibly more effective than at larger, more spaced colonies. In addition, no other avian species nested on South Conjers because the island is so small. In contrast, Laughing Gulls, Herring Gulls, and Greater Black-backed Gulls nested in or around colonies at Wire Narrows and Man & Boy. However, North and South Conjers islands are only 300 m apart and so size of colony and density of nests as a factor in warding off predation may have been the most important factor. As further support for this, predated Common Tern nests at Wire Narrows West, Wire Narrows East, and Man & Boy were farther apart than nests not predated (although only significantly at Wire Narrows West).

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 do not treat Ruddy Turnstones as predators. 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). None of the birds chased the Ruddy Turnstones away when they were eating eggs.

Hatched nests were closer together than unsuccessful nests for Common Terns and Black Skimmers. It is possible that birds nesting in denser areas were able to deter predators more effectively. However, this relationship only held true at the Wire Narrows shellpiles. DiCostanzo (1980) found that older birds were the nucleus of the colony, and it is possible that nests in high density areas were nests of older, experienced breeders.

Hatching Success Summary

Overall, hatching success was low on the shellpiles. Erwin (1977b) found hatching success in Black Skimmers on barrier islands in Virginia to be close to 80%, while Burger and Gochfeld (1990) found a hatching success rate of 54% on marsh islands in New Jersey. Only 45% of Black Skimmers nests on shellpiles hatched. 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% on the shellpiles. 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. Eyler et al. (1999) found that hatching success for Gull-billed Terns was lower on marsh islands (54% hatched) than barrier island beaches (72% hatched). Fifty-four percent of Gull-billed Terns hatched in this study, although the hatching success was very low (less than 15% hatched) on 2 of the 3 shellpiles they used.

The multiple regression analysis found, across species and shellpiles, that elevation and date of nest-initiation explain the most variation in hatching success. Clutch and nearest-neighbor distance were significant contributors to the model at some shellpiles, but not all. Since date of nest-initiation strongly affected hatching success because the floods of early June caused low nest success in the early season, 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. The choice of a nest site by birds nesting on the shellpiles, therefore, is not based on 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 low-lying 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) found lower flooding rates and higher hatching success on barrier island beaches than on marsh shellpiles. Because flooding due to high tides is unpredictable and water levels reach different heights each year, the low nest sites may reflect a trade-off between nesting above flood tide lines and nesting on preferred substrates.

Sea Level Rise

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. If sea levels rise and no new accumulation of shell on the piles occur, then the shellpiles will be completely inundated and unsuitable as colony sites. As the number of floods washing away nests increases over the years, the number of birds in the colonies will likely decrease. Since barrier island beaches have become unsuitable colony sites due to the presence of mammalian predators (Erwin et al. 2001), most breeding habitats in Virginia in the future may be “sinks” rather than “sources”. However, the shellpiles are storm deposited and the frequency of storms is predicted to increase with global warming, so new accumulation of shell may occur.

Management Implications

The objective of this study was to determine how experimentally elevating shellpiles affects nest-site choice and hatching success of the four focal species. I expected higher elevation sites would be selected for nest-sites because of their increased protection from flooding, and thus would increase breeding success. The elevated sites did provide extra protection from flooding; however, the birds did not select these sites preferentially because factors other than elevation appeared to be more important in nest-site selection. In order to effectively manage colony sites to reduce flooding, it is important to understand the factors important in habitat selection.

Since flooding was the major cause of nest failure in this study, and because sea levels are expected to rise, management of low-lying colony sites is still an important objective. Based on the data collected in this study, a number of improvements to the design of this project can be made. First, if elevated plots were located in specific places where birds were known to have nested in previous years, and to have been flooded, selection of nest-sites on elevated plots may increase. For example, if an elevated plot was located on the low ridge on Man & Boy where Gull-billed Terns nested, and flooded, hatching success may improve. An elevated plot of 20-30 cm would have protected these nests from flooding. Because plots were located randomly within areas that were used, the plots were not located where densest aggregation of nests was found. At Wire Narrows West, an elevated plot in an area where many Common Tern nests failed would only have to provide 15 cm extra shell height to protect nests from flooding. Larger elevated plots or plots closer together may also attract more birds because of the importance of social attraction in nest-site selection for colonial species. In addition, stabilizing the elevated plots so that waves cannot erode edges of the plots would help the success of the plots, especially in the lower-lying areas where many Common Terns nest.

Second, putting wrack over selected elevated plots may encourage more birds, especially Common Terns, to nest at higher elevations. Placing wrack on higher, protected areas of the shellpile that were not flooded in 2002 may also work to attract birds to higher sites. At North Conjers wrack covered most of the area used by Common Terns and this was the only shellpile where the wrack nests had the highest elevations of all substrates.

Third, planting of short, sparse vegetation or placement of shade-providing objects on the shellpile may also attract birds to higher sites. At Wire Narrows West and East nests surrounded one small plant at a high elevation over the course of the season (6 nests at WNE, 7 at WNW). At Wire Narrows West the plant died before the end of the season, but at Wire Narrows East 5 chicks were counted using the plant as shelter on a hot day. Providing a few small plants or other sources of shade in key elevated areas may attract birds to more protected areas.

Finally, if Laughing Gulls deter birds from nesting on more protected sites near the marsh boundary, discouraging nesting of gulls around the shellpile may also increase use of areas of the shellpile not affected by flooding. This may also improve reproductive success if laughing gulls take a significant number of eggs and chicks off the shellpiles.

Conclusions

The elevation of a nest had the most influence on its success. Despite this, the majority of nesting pairs of all four species did not select experimentally elevated plots for nest-sites. Late nests had higher hatching success than early nests at most shellpiles, primarily because the major flooding occurred in early June. Predation rates over the course of the season were relatively even. However, a high percentage of very early nests were destroyed by Ruddy Turnstone predation. Despite the failure of the elevated sites to attract nesting birds, the sites were protected from flooding. Because sea level rise is an imminent threat to nesting waterbirds off the coast of Virginia, management of nesting sites to reduce flooding is still necessary.

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Appendix 1. Experimental plot elevations at 5 shellpile sites.

Wire Narrows West Plots	High Point Elevation (m)	Average Difference (cm)
1E	1.3	14.5
1C	1.15	
2E	1.27	12.5
2C	1.14	
3E	1.27	14
3C	1.13	
4E	1.4	16.5
4C	1.31	
5E	1.33	9.7
5C	1.25	
6E	1.4	19.5
6C	1.21	

Man & Boy Plots	High Point Elevation (m)	Average Difference (cm)
1E	1.65	8.5
1C	1.56	
2E	1.63	10
2C	1.53	
3E	1.73	24.3
3C	1.50	
4E	1.53	18.5
4C	1.33	
5E	1.73	21.3
5C	1.52	
6E	1.27	13.5
6C	1.14	

Wire Narrows East Plots	High Point Elevation (m)	Average Difference (cm)
1E	1.42	13.5
1C	1.26	
2E	1.47	15
2C	1.26	
3E	1.5	14.3
3C	1.37	
4E	1.54	14.5
4C	1.36	
5E	1.62	17.7
5C	1.38	
6E	1.32	17.5
6C	1.11	

North Conjers Plots	High Point Elevation (m)	Average Difference (cm)
1E	1.75	22
1C	1.53	
2E	1.62	18
2C	1.44	
3E	1.48	8.25
3C	1.44	
4E	1.70	13
4C	1.57	
5E	1.75	17
5C	1.58	
6E	1.32	13.7
6C	1.19	

Elevated Differences (cm)	
Overall Average:	15.9
Man&Boy:	16.0
North Conjers	15.3
South Conjers	19.1
Wire Narrows West	14.5
Wire Narrows East	15.4

South Conjers Plots	High Point Elevation (m)	Average Difference (cm)
1E	1.47	14.5
1C	1.51	
2E	1.9	32
2C	1.63	
3E	1.79	17
3C	1.58	
4E	1.39	13
4C	1.26	

Appendix 2. Experimental plot longevity at 5 shellpiles sites.

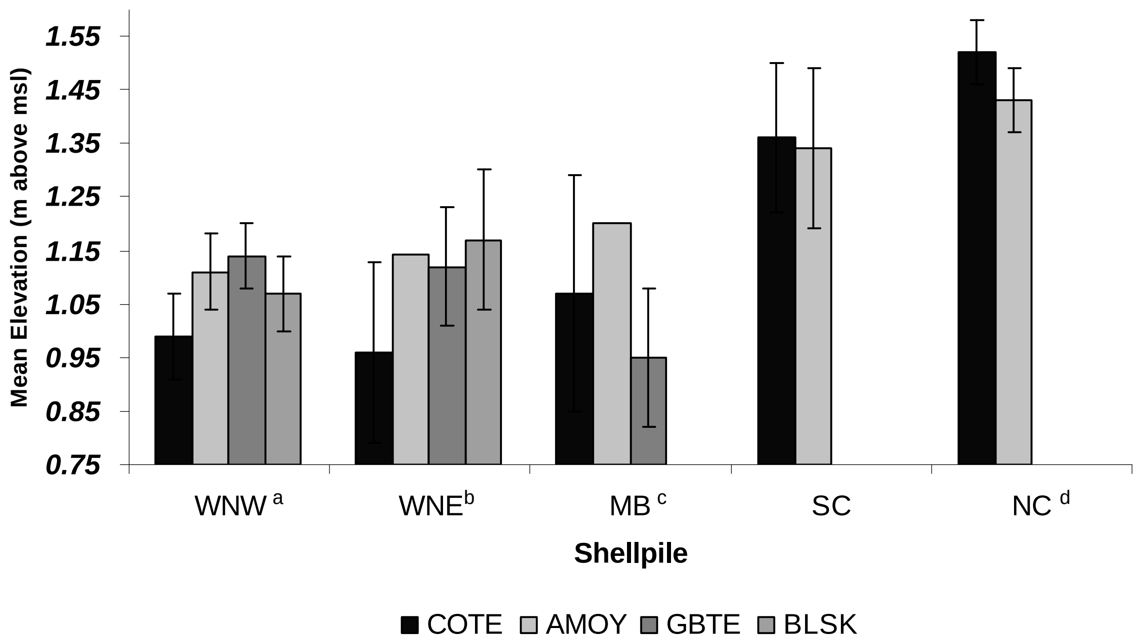
Wire Narrows West	
Plot 1C	intact
Plot 1E	intact
Plot 2C	intact
Plot 2E	intact
Plot 3C	intact
Plot 3E	intact
Plot 4C	100% new shell;no erosion
Plot 4E	100% new shell;no erosion
Plot 5C	100% new shell;no erosion
Plot 5E	100% new shell;no erosion
Plot 6C	intact
Plot 6E	intact

Wire Narrows East	
Plot 1C	30% eroded
Plot 1E	30% eroded
Plot 2C	intact
Plot 2E	intact
Plot 3C	gone
Plot 3E	gone
Plot 4C	50% new shell
Plot 4E	50% new wrack
Plot 5C	50% eroded
Plot 5E	50% eroded
Plot 6C	intact
Plot 6E	intact

Man & Boy	
Plot 1C	intact
Plot 1E	intact
Plot 2C	intact
Plot 2E	intact
Plot 3C	1/3 cut away
Plot 3E	intact
Plot 4C	1/2 new wrack
Plot 4E	intact
Plot 5C	1/3 cut away
Plot 5E	1/3 cut away
Plot 6C	intact
Plot 6E	intact

North Conjers	
Plot 1C	flooded
Plot 1E	intact
Plot 2C	flooded
Plot 2E	intact
Plot 3C	flooded
Plot 3E	intact
Plot 4C	flooded
Plot 4E	intact
Plot 5C	flooded
Plot 5E	intact
Plot 6C	flooded
Plot 6E	intact

South Conjers	
Plot 1C	100% overwash
Plot 1E	overwash & reshaped
Plot 2C	repeatedly flooded
Plot 2E	intact
Plot 3C	100% flooded
Plot 3E	30% cut away
Plot 4C	flooded
Plot 4E	intact



Appendix 3. Differences in nest elevations between species at each shellpile.

a: WNW ANOVA F=54.65, P<0.001. GBTE higher than BLSK and COTE, AMOY higher than COTE, and BLSK higher than COTE all at P=0.05 using Tukey's studentized range test.

b: WNE ANOVA, F=11.38, P<0.001. BLSK and GBTE higher than COTE at P=0.05 using Tukey's studentized range test.

c: MB T=2.08, P=0.04, GBTE lower than COTE.

d: NC T=-3.15, P=0.002, COTE higher than AMOY.

Appendix 4. Substrate and exposure use at 5 shellpile sites. Shown is % in each category and results from chi-square analysis on contingency table.

Wire Narrows West

	Exposed	Neutral	Total
Shell-Wrack	11	4	14
Shell	10	32	41
Wrack	38	6	44
Total	59	41	n=311

?2=111.69, P<0.001

Wire Narrows East

	Exposed	Neutral	Total
Shell-Wrack	14	7	21
Shell	8	15	23
Wrack	50	7	56
Total	71	29	n=177

?2=40.03, P<0.001

Man &Boy

	Exposed	Protected	Neutral	Total
Shell-Wrack	13	7	33	53
Shell	8	1	14	23
Wrack	14	6	4	24
Total	35	14	51	n=189

?2=28.46, P<0.001

South Conjers

	Exposed	Neutral	Total
Shell-Wrack	24	10	34
Shell	11	19	30
Wrack	27	9	36
Total	62	38	n=97

?2=10.19 , P<0.001

North Conjers

	Exposed	Neutral	Total
Shell-Wrack	7	10	17
Shell	3	17	20
Wrack	3	60	63
Total	23	87	n=30

sample size not large enough for analysis

Appendix 5. Substrate and exposure use for each species with all shellpiles combined. Shown is % in each category and results of chi-square analysis on contingency table.

GBTE	Exposed	Neutral	Total
Shell-Wrack	7	17	25
Shell	7	62	69
Wrack	1	5	6
Total	16	84	n=81

not significant

COTE	Exposed	Neutral	Total
SW	16	15	31
Shell	7	11	18
Wrack	39	12	51
Total	62	38	n=628

?2=66.1, P<0.001

BLSK	Exposed	Neutral	Total
SW	1	7	8
Shell	13	61	75
Wrack	11	7	17
Total	25	75	n=75

?2=10.9, P=0.004

AMOY	Exposed	Neutral	Total
SW	0	5	5
Shell	37	58	95
Wrack	0	0	0
Total	37	63	n=19

sample size not large enough for analysis

Appendix 6. Substrate use and nest-initiation date for 3 waterbird species.

					Substrate	
Site	**Species**	**Time**	**n**	**% Shell-Wrack**	**% Shell**	**% Wrack**
WNW						
	COTE					
		Early	111	14	21	65
		Late	84	25	12	63
	GBTE[a]					
		Early	17	18	82	0
		Late	30	0	100	0
	BLSK					
		Early	55	11	67	22
		Late	66	0	91	9
WNE						
	COTE[a]					
		Early	83	10	8	82
		Late	66	16	20	44
MB						
	COTE					
		Early	90	47	23	30
		Late	79	57	24	19
SC						
	COTE[a]					
		Early	42	21	24	55
		Late	57	42	33	25
NC						
	COTE					
		Early	10	20	0	80
		Late	13	15	0	85

Chi-square analysis on contingency table to compare substrate use between early and late nests.

a: WNW-GBTE ?2=5.66, P=0.02; WNE-COTE ?2=23.85, P<0.001; SC-COTE ?2=9.76, P=0.008.

Appendix 7. Exposure of nest and nest-initation date.

Site	Species	Time	n	Exposure % exposed	% neutral	% protected	
WNW							
	COTE						ns
		Early	109	78	22		
		Late	84	88	12		
	GBTE						ns
		Early	17	12	88		
		Late	30	0	100		
	BLSK						ns
		Early	54	30	70		
		Late	11	18	82		
WNE							
	COTE						*
		Early	83	81	19		
		Late	66	64	36		
MB							
	COTE						**
		Early	90	43	37	20	
		Late	79	32	68	0	
SC							
	COTE						ns
		Early	38	58	42		
		Late	57	63	37		
NC							
	COTE						ns
		Early	10	10	90		
		Late	13	15	85		

Chi-square analysis on contingency table to compare exposure levels between early and late nests. More nests on neutral sites in
*WNE-COTE ?2=5.47, P=0.02.
**MB-COTE ?2=25.52, P<0.001.

Appendix 8. Nearest-neighbor results for 4 waterbird species at 5 shellpile sites.

Site	Species	Distance to:	n	average distance (m ± 1 SD)
Wire Narrows West				
	COTE	COTE	179	1.12 ± .79
		GBTE	179	8.26 ± 6.87
		BLSK	179	5.75 ± 5.03
		nearest*	179	1.004 ± .65
	GBTE	GBTE	47	1.15 ± .93
		COTE	47	1.49 ± .79
		BLSK	47	3.7 ± 5.05
		nearest	47	0.78 ± .37
	BLSK	BLSK	59	2.79 ± 8.49
		COTE	59	1.74 ± 1.24
		GBTE	59	3.51 ± 6.26
		nearest	59	0.92 ± .78
	AMOY	nearest	5	30.62 ± 24.1
Wire Narrows East				
	COTE	COTE	113	1.2 ± .87
		GBTE	94	17.47 ± 27.3
		BLSK	28	32.02 ± 35
		nearest	115	1.17 ± .84
	GBTE	GBTE	15	6.23 ± 19.35
		COTE	3	71.7 ± 1.55
		nearest	15	6.06 ± 18.64
	BLSK	BLSK	6	1.6 ± .62
		COTE	7	1.17 ± .49
		nearest	7	0.92 ± .27
Man & Boy				
	COTE	COTE	150	1.65 ± 1.68
		GBTE	150	10.82 ± 7.27
		AMOY	17	20.1 ± 7.15
		nearest	150	1.57 ± 1.55
	GBTE	GBTE	16	3.4 ± 7.04
		COTE	16	2.4 ± 1.1
		nearest	16	0.88 ± .54
South Conjers				
	COTE	COTE	89	1.21 ± .92
		AMOY	70	8.41 ± 3.93
		nearest	89	1.21 ± .92
	AMOY	nearest	5	7.83 ± 4.3
North Conjers				
	AMOY	nearest	7	21.12 ± 11.83

*distance to nearest nest of any species

Appendix 9. Summary of nest outcomes at Wire Narrows West

	# nests	% of total	# early nests	% of nests for species	# late nests	% of nests for species
COTE	197	63	112	57	85	43
GBTE	47	15	17	36	30	64
BLSK	66	21	55	83	11	17
AMOY	5	2	3	60	2	40
Total	315	100	187	59	128	41

Common Tern Nest Outcomes at Wire Narrows West

	n	% hatched	% probable hatch	% total hatch	% predated	% flooded	% abandoned	% unknown fail	% total fail	% unknown outcome
Early	112	11	13	24	11	57	4	0	72	4
Late	85	42	25	67	7	2	1	11	21	12
Total	197	24	18	43	9	34	3	5	50	7

Gull-billed Tern Nest Outcomes at Wire Narrows West

		% hatched	% probable hatch	% total hatch	% predated	% flooded	% abandoned	% unknown fail	% total fail	% unknown outcome
Early	17	82	0	82	18	0	0	0	18	0
Late	30	67	17	83	10	0	0	7	17	0
Total	47	72	11	83	13	0	0	4	17	0

Black Skimmer Nest Outcomes at Wire Narrows West

		% hatched	% probable hatch	% total hatch	% predated	% flooded	% abandoned	% unknown fail	% total fail	% unknown outcome
Early	55	38	4	42	18	11	15	2	45	13
Late	11	27	9	36	36	0	0	18	55	9
Total	66	36	5	41	21	9	12	5	47	12

American Oystercatcher Nest Outcomes at Wire Narrows West

		% hatched	% probable hatch	% total hatch	% predated	% flooded	% abandoned	% unknown fail	% total fail	% unknown outcome
Early	3	33	33	66	0	0	0	0	0	33
Late	2	50	0	50	50	0	0	0	50	0
Total	5	40	20	60	20	0	0	0	20	20

Appendix 10. Summary of Nest Outcome at Wire Narrows East

	# nests	% of total	# early nests	% of nests for species	# late nests	% of nests for species
COTE	148	84	82	55	66	45
GBTE	18	10	16	89	2	11
BLSK	9	5	2	22	7	78
AMOY	1	1	1	100		
CATE	1	1	1	100		
Total	177	100	102	58	75	42

Common Tern Nest Outcomes at Wire Narrows East

	n	% hatched	% probable hatch	% total hatch	% predated	% flooded	% abandoned	% unknown fail	% total fail	% unknown outcome
Early	82	6	2	9	4	85	0	0	91	2
Late	66	55	20	74	8	2	0	5	26	12
Total	148	28	10	38	5	48	0	2	55	7

Gull-billed Tern Nest Outcomes at Wire Narrows East

		% hatched	% probable hatch	% total hatch	% predated	% flooded	% abandoned	% unknown fail	% total fail	% unknown outcome
Early	16	12	0	12	75	13	0	0	88	0
Late	2	0	0	0	100	0	0	0	100	0
Total	18	11	0	11	78	11	0	0	89	0

Black Skimmer Nest Outcomes at Wire Narrows East

		% hatched	% probable hatch	% total hatch	% predated	% flooded	% abandoned	% unknown fail	% total fail	% unknown outcome
Early	2	0	0	0	0	100	0	0	100	0
Late	7	29	14	43	0	0	0	43	43	14
Total	9	22	11	33	0	22	0	33	56	11

American Oystercatcher Nest Outcomes at Wire Narrows East

		% hatched	% probable hatch	% total hatch	% predated	% flooded	% abandoned	% unknown fail	% total fail	% unknown outcome
Early	1	0	0	0	0	0	0	0	0	100
Late	0	0	0	0	0	0	0	0	0	0
Total	1	0	0	0	0	0	0	0	0	100

Appendix 11. Summary of Nest Outcome at Man & Boy

	# nests	% of total	# early nests	% of nests for species	# late nests	% of nests for species
COTE	169	89	90	53	79	47
GBTE	16	8	14	88	2	13
AMOY	1	1	1	100	0	0
Unk	3	2	3		0	
Total	189	100	108	57	81	43

Common Tern Nest Outcomes at Man & Boy

	n	% hatched	% probable hatch	% total hatch	% predated	% flooded	% abandoned	% unknown fail	% total fail	% unknown outcome
Early	90	24	3	28	14	52	1	0	68	4
Late	79	51	9	60	13	0	9	3	24	16
Total	169	37	6	43	14	28	5	1	47	10

Gull-billed Tern Nest Outcomes at Man & Boy

	n	% hatched	% probable hatch	% total hatch	% predated	% flooded	% abandoned	% unknown fail	% total fail	% unknown outcome
Early	14	13	0	13	19	56	0	0	87	0
Late	2	0	0	0	0	0	100	0	100	0
Total	16	13	0	13	19	56	13	0	87	0

American Oystercatcher Nest Outcomes at Man & Boy

	n	% hatched	% probable hatch	% total hatch	% predated	% flooded	% abandoned	% unknown fail	% total fail	% unknown outcome
Early	1	0	0	0	0	0	0	0	0	100
Late	0	0	0	0	0	0	0	0	0	0
Total	1	0	0	0	0	0	0	0	0	100

Appendix 12. Summary of Nest Outcome at South Conjers

	# nests	% of total	# early nests	% of nests for species	# late nests	% of nests for species
COTE	95	95	38	40	57	60
AMOY	5	5	4	80	1	20
Total	100	100	42	42	58	58

Common Tern Nest Outcomes at South Conjers

	n	% hatched	% probable hatch	% total hatch	% predated	% flooded	% abandoned	% unknown fail	% total fail	% unknown outcome
Early	38	13	0	13	3	71	8	0	82	5
Late	57	25	26	51	4	30	7	4	44	5
Total	95	20	16	36	3	46	7	2	59	5

American Oystercatcher Nest Outcomes at South Conjers

	n	% hatched	% probable hatch	% total hatch	% predated	% flooded	% abandoned	% unknown fail	% total fail	% unknown outcome
Early	4	0	25	0	0	50	0	0	50	25
Late	1	0	100	100	0	0	0	0	0	0
Total	5	0	40	40	0	40	0	0	40	20

Appendix 13. Summary of Nest Outcome at North Conjers

	# nests	% of total	# early nests	% of nests for species	# late nests	% of nests for species
COTE	23	77	10	43	13	57
AMOY	7	23	7	100	0	0
Total	30	100	17	57	13	43

Common Tern Nest Outcomes at North Conjers

	n	% hatched	% probable hatch	% total hatch	% predated	% flooded	% abandoned	% unknown fail	% total fail	% unknown outcome
Early	10	20	0	20	50	30	0	80	0	0
Late	13	23	23	46	15	0	8	15	39	15
Total	23	22	13	35	31	13	4	9	57	9

American Oystercatcher Nest Outcomes at North Conjers

	n	% hatched	% probable hatch	% total hatch	% predated	% flooded	% abandoned	% unknown fail	% total fail	% unknown outcome
Early	7	0	14	14	43	14	0	14	71	14
Late	0	0	0	0	0	0	0	0	0	0
Total	7	0	14	14	43	14	0	14	71	14

Appendix 14. Tide Data for Dates of Nest Flooding in 2002

all data in meters

Date	Predicted HH[a]	Actual HH[b]	Actual - Predicted	1979-2001 HH[c]	Average HH 1979-2001[d]	# nests flooded
25-May	1.65	1.59	-0.06	1.86	1.51	
26-May	1.65	1.72	0.08	1.85	1.54	17
27-May	1.62	1.68	0.06	1.81	1.52	
28-May	1.55	1.59	0.04	1.73	1.48	
05-Jun	1.28	1.19	-0.09	1.84	1.49	
06-Jun	1.34	1.26	-0.08	1.94	1.47	
07-Jun*	1.40	1.85	0.45	1.86	1.47	199
08-Jun	1.46	1.65	0.19	1.70	1.47	
10-Jun	1.49	1.47	-0.03	1.79	1.53	
11-Jun	1.49	1.52	0.03	1.88	1.51	14
12-Jun	1.49	1.49	0.00	1.93	1.53	
13-Jun	1.49	1.54	0.04	1.98	1.54	
14-Jun*	1.49	1.89	0.39	1.81	1.54	14
15-Jun	1.43	1.79	0.36	1.80	1.49	
16-Jun	1.43	1.70	0.27	1.90	1.48	
17-Jun	1.40	1.57	0.16	1.60	1.46	
18-Jun	1.34	1.45	0.11	1.75	1.49	2
19-Jun	1.40	1.38	-0.02	1.66	1.48	
20-Jun	1.46	1.30	-0.16	1.74	1.48	
08-Jul	1.49	1.36	-0.14	1.65	1.48	
09-Jul	1.52	1.44	-0.08	1.76	1.49	
10-Jul	1.55	1.40	-0.16	1.80	1.52	
11-Jul	1.55	1.59	0.04	1.81	1.53	14 at South Conjers
12-Jul	1.55	1.72	0.17	1.87	1.55	
13-Jul	1.52	1.58	0.05	2.03	1.53	
14-Jul	1.46	1.55	0.09	1.82	1.48	
18-Jul	1.43	1.54	0.11	1.75	1.50	
19-Jul	1.46	1.54	0.08	1.75	1.49	

*June 7-14: Dates of major flooding; 57% of nests lost this week, most on June 7th

a: predicted tide data from Wachapreague Channel from VIMS, 2002

b:actual tide data from NOAA 2002, Wachapreague Channel

c:Highest high above mean lowest low water for 1979-2001 Wachapreague Channel (NOAA 2002) for each day

d: Average highest high above mean lowest low water for each day, 1979-2001 Wachapreague Channel, NOAA 2002