

## ABSTRACT

SCHULTE, SHILOH AUTUMN. Ecology and Population Dynamics of American Oystercatchers (*Haematopus palliatus*). (Under the direction of Theodore R. Simons.)

Coastal ecosystems are under increasing pressure from multiple sources, including human activity, introduced species, and effects of climate change. American Oystercatchers (*Haematopus palliatus*) are large shorebirds that are strictly tied to the temperate coastal zone throughout the year. I studied the reproductive ecology, population dynamics, and migratory patterns of American Oystercatchers on the Outer Banks of North Carolina from 2004 through 2008. This work was part of a long term study of Oystercatchers initiated in 1997. I took an information-theoretic approach to analyzing factors affecting the survival of Oystercatcher nests and broods. I evaluated survival with respect to nesting island, year, time of season, brood age, distance to tide, presence of off road vehicles, and proximity of foraging habitat. Model results indicate direct access to foraging sites has a positive effect on brood survival, while off road vehicles have a negative effect. I studied chick behavior and survival using radio telemetry and direct observation and found that chicks on beaches closed to vehicles used beach and intertidal zones more frequently than chicks on beaches open to vehicles (34 min/hr vs 15 min/hr). I identified the source of mortality for 37 radio-tagged chicks. Six (16%) were killed by vehicles, 21 (57%) by predators, and 10 (27%) by exposure and starvation. Chick predators included Great Horned Owls (*Bubo virginianus*) Fish Crows (*Corvus ossifragus*), Feral Cats (*Felis catus*), Mink (*Mustela vison*), Raccoons (*Procyon lotor*), and Ghost Crabs (*Ocypode albicans*).

I compared alternative nest survival models to find the best explanation for changes in nest survival in relation to periodic hurricane events. Nesting success increased from 20%, to 80% on Cape Lookout National Seashore after Hurricane Isabel crossed the island in 2003. I compared nest survival in open flat and vegetated dune habitats on two barrier islands and measured the extent of the habitat change after the storm. Both islands experienced extensive habitat change during the storm, but nest survival only increased on the island with an apparent reduction in predator activity. When overall nest survival was high or low there was no observed effect of nest placement on nest survival. At intermediate levels nests on open flats survived at a higher rate than nests placed in dunes. Periodic years with elevated nest survival can help compensate for low annual productivity and may be important for the growth and stability of Oystercatcher populations.

I used mark-recapture and nest survival data from this study and from literature sources to develop a demographic model for the American Oystercatcher population in North Carolina and assess the effects of periodic hurricanes on population growth. I constructed a baseline stochastic population model without hurricane effects and two alternative parameter sets based on hurricane strike probabilities for North Carolina counties (10 and 15 year hurricane events). The baseline model had the lowest growth rate ( $\lambda = 0.986$ ), while both models that included hurricanes predicted an increasing population. These results suggest that American Oystercatcher life history strategies may have been shaped by periodic hurricane disturbance events that improve habitat and reduce predator populations

I quantified Oystercatcher migration patterns and site fidelity through an analysis of eight years of range-wide mark-recapture data. I found that migration probability declined

from North to South, and that northern breeders tend to employ a “leapfrog” strategy and bypass mid-Atlantic sites to concentrate in southern wintering sites, notably the West coast of Florida. Oystercatchers display strong site fidelity to both breeding and wintering sites, with approximately 90% returning to the same sites annually. Current ad-hoc or localized mark-resight efforts limit our ability to maximize the potential of the cooperative marking effort. Coordinated ongoing breeding season resight surveys combined with periodic winter surveys will allow us to track spatial and temporal changes in survival, recruitment, reproductive success, and migratory patterns.

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Ecology and Population Dynamics of American Oystercatchers  
(*Haematopus palliatus*)

by  
Shiloh Autumn Schulte

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## **DEDICATION**

This dissertation is dedicated to my incredibly patient, intelligent, motivated, and caring wife, Shevaun Bateman Schulte, and to our wonderful daughters, Lorien and Caelyn Schulte.

## **BIOGRAPHY**

I was born in Dover, New Hampshire on October 5<sup>th</sup> 1978. I was the third in line in a family of five kids. Growing up in Jericho, Vermont I spent as much time as possible roaming the woods and fields near our house. I quickly developed a fascination with the natural world and with birds in particular. My siblings and I were homeschooled by my parents, Bill and June Schulte. My parent's style of teaching encouraged self motivation and direction while allowing for a great deal of flexibility in pursuing my interests. By the time I enrolled at the University of Vermont as a Wildlife Biology major in 1996 I was convinced that I wanted a career as a wildlife biologist. This goal was supported by my undergraduate advisors Dr. David Hirth and Dr. David Capen who encouraged me to find seasonal work on research projects early on. I was lucky enough to find a summer field tech job on the North Slope of Alaska after my freshman year. This experience fueled my motivation to keep on the path of fieldwork and research and subsequent field seasons found me in Alaska, Colorado, Washington, Vermont, and Northern Maine.

While at the University of Vermont I practiced Tae Kwon Do and reached the rank of 2<sup>nd</sup> Dan (black belt), became a leader in the Outing Club, and most importantly, met Shevaun Bateman. Shevaun and I married in 2003, three years after I graduated.

My introduction to the world of Oystercatchers came about when I took a job with the Manomet Center for Conservation Sciences working with Stephen Brown and Brian Harrington on an aerial survey of the species in North America. Through this project I met a number of very smart and dedicated people working to understand and conserve this unique species. One of those people, Ted Simons, had a doctoral position open at NCSU to study

Oystercatchers on the Outer Banks of North Carolina. In 2004 Shevaun and I moved to Raleigh and I spent the next five years roaming the Outer Banks and teaching undergraduates. In 2009 I again had the opportunity to take a position at Manomet organizing a conservation effort to recover Oystercatcher populations at the continental scale. For three years I balanced work, family, and dissertation writing. Along the way we welcomed Lorien Schulte and Caelyn Schulte into the world and discovered the immense joys and fears that come with parenting.



## ACKNOWLEDGMENTS

This dissertation is the culmination of many years of hard work, stress, contemplation, inspiration, support and sacrifice by many people. I first want to thank my wife, Shevaun Schulte, and my daughters, Lorien and Caelyn. You are a constant source of love and support and a reminder of the priorities in life. To my parents, Bill and June Schulte, thank you for always believing I am doing something worthwhile with my life.

To my advisor, Ted Simons, thank you for your guidance, patience, support and knowledge over the course of my graduate career. You gave me an amazing opportunity and did everything you could to help me make the most of it.

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My graduate school experience was shaped in large part by my fellow grad students and post-docs. I want to especially thank Becky Hylton Keller, Conor McGowan, Krishna Pacifici, Jerome Brewster, Nathan Tarr, Arielle Waldstein, Marybeth Brey, Tom Riddle, Jessica Stocking, Tracey Borneman, and Sarah Friedl.

Finally, thanks to the people that worked hard every year to collect data and protect Oystercatchers on the Outer Banks of North Carolina. Jeff Cordes, Michael Rikard, Jon Altman, Karen Sayles, Marcia Lyons, Britta Muiznieks, Doug McGee, and the vast and dedicated army of seasonal field techs

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**Chapter 1.**

**Factors affecting the reproductive success of American Oystercatchers in North  
Carolina**

Abstract:

I took an information-theoretic approach to the analysis of factors affecting the survival of American Oystercatcher (*Haematopus palliatus*) nests and broods on the Outer Banks of North Carolina. I evaluated survival with respect to nesting island, year, time of season, brood age, distance to tide, presence of off road vehicles, and proximity of foraging habitat. The daily nest survival (mean 0.981, SE 0.002) was affected by year and island, and declined over the nesting season. Mammals were responsible for 54% of identified nest failures. Daily brood survival (mean 0.981, SE 0.002) varied by island and increased non-linearly with age, with highest mortality within 7 days after hatch. Model results indicate direct access to foraging sites has a positive effect on brood survival, while off road vehicles have a negative effect. I studied chick behavior and survival using radio telemetry and direct observation and found that vehicles caused mortality and affected behavior and resource use of Oystercatcher chicks. I identified the source of mortality for 37 radio-tagged chicks. Six (16%) were killed by vehicles, 21 (57%) by predators, and 10 (27%) by exposure and starvation. From 1995-2008 twenty-five additional Oystercatcher chicks were found dead. Thirteen (52%) were killed by vehicles. Chicks on beaches closed to vehicles used beach and intertidal zones more frequently than chicks on beaches open to vehicles (34 min/hr vs 15 min/hr). Chick predators included Great Horned Owls (*Bubo virginianus*) Fish Crows (*Corvus ossifragus*), Feral Cats (*Felis catus*), Mink (*Mustela vison*), Raccoons (*Procyon lotor*), and Ghost Crabs (*Ocypode albicans*).

## Introduction:

American Oystercatchers (*Haematopus palliatus*) are large, conspicuous shorebirds that are strictly tied to the coastal zone throughout the year. Unlike many shorebirds that breed in the Arctic and migrate to coastal regions in the winter, Oystercatchers breed along the Atlantic Coast from Nova Scotia to Florida, and along the Gulf Coast from Florida to Mexico (Nol and Humphrey 1994). The winter range extends from central New Jersey south through the Gulf of Mexico. An aerial survey of the species' winter range resulted in a population estimate of 10971 individuals (+/-298), with 7500-8000 wintering on the Atlantic Coast (Brown et al. 2005). The survey estimated a winter population of Oystercatchers in North Carolina at 647 birds. A 2007 breeding season survey estimated North Carolina's summer population at 717 individuals, with 339 breeding pairs (Cameron and Allen 2007).

American Oystercatchers are listed in both Georgia and Florida as "threatened", and as a "species of special concern" in North Carolina (North Carolina Wildlife Resources Commission 2008). The American Oystercatcher Conservation Plan lists American Oystercatchers as a high priority species (American Oystercatcher Working Group, 2007), in part because of significant threats from development and heavy recreational use of coastal breeding habitats. Human population density in the United States is highest in coastal regions. The rate of population growth is expected to increase substantially, particularly in the southeastern states (Crossett et al. 2004). As more humans inhabit the coastal zone, recreational use of beaches, salt marshes, and waterways will continue to rise as well. Many visitors to the coast seek out undeveloped beaches. As coastal islands and beaches are developed, more visitors are concentrated onto the remaining undeveloped areas. Coastal

development, recreational activity, and altered predator communities have substantially reduced the amount of suitable nesting and foraging habitat for beach nesting birds in North Carolina. Roads and artificial dunes along nesting beaches can limit access to foraging habitats for beach nesting species like Piping Plovers (*Charadrius melodus*) and American Oystercatchers. Nesting and roosting sites can also be lost when jetties and revetments alter the normal process of longshore transport of sand and accelerate erosion of adjacent beaches.

Like many long-lived species, Oystercatcher reproductive rates tend to be highly variable but generally low (Evans 1991, Nol and Humphrey 1994, Davis et al. 2001, Wilke et al. 2005, McGowan et al. 2005a, Traut et al. 2006). This means that the species is unable to recover quickly from population declines. These traits also make it difficult to assess the status of a population because populations can persist for many years, even if reproductive success is low. Surveys indicate that populations in the Mid-Atlantic States are declining (Mawhinney and Benedict 1999, Nol et al. 2000, Davis et al. 2001). The breeding population of Virginia's barrier islands, a historical stronghold for Oystercatchers, fell from 619 breeding pairs in 1979 to 255 breeding pairs in 1998 (Davis et al. 2001). A 2004 survey that covered the same region estimated the population at 302 breeding pairs (Wilke et al. 2005). This survey also covered lagoon and marsh habitat and found an additional 223 pairs. These results and earlier work (Lauro and Burger 1989) suggest populations may be moving into non-traditional habitats, and highlight the need for additional surveys in marsh and upland habitats not normally associated with Oystercatchers. During the period of apparent decline in the mid-Atlantic, the species expanded its breeding range into the northeastern United States (Davis 1999, Mawhinney and Benedict 1999, Nol et al. 2000, Davis et al.

2001). Understanding the causes of local, regional, and continental population trends will require studies of the species' population structure and demographics at the coastal scale.

A study of breeding American Oystercatchers was initiated on South Core Banks, Cape Lookout National Seashore in 1995 to document nesting success (Novick 1996). The scope of the original study has expanded to include all of the islands of Cape Lookout and Cape Hatteras National Seashores. The study of Oystercatcher breeding success further expanded in the state in 2002 and 2003 when the North Carolina Audubon Society initiated nest monitoring on dredge spoil islands at the mouth of the Cape Fear River, and on Lea and Hutaff Islands. Although the undeveloped barrier islands that comprise the National Seashores were thought to be ideal breeding habitat for American Oystercatchers, nest survival was much lower than expected. Novick (1996) attributed low hatching rates to human disturbance. Davis (1999) continued the work on Cape Lookout and used nest monitoring and predator tracking stations to determine the causes of nest failure. Davis determined that a majority of nests were lost to mammalian predators. Subsequent studies in North Carolina have supported the conclusion that mammals are the primary nest predators, but they also suggested an interaction between human disturbance and nest predation rates (McGowan 2004, McGowan and Simons 2006). McGowan and Simons (2006) found an inverse relationship between the number of visits an Oystercatcher made to the nest and the nest survival rate, suggesting that more disturbed nests are more likely to be found by predators.

Although a considerable amount of research has been conducted on nesting American Oystercatchers, relatively few studies have focused on chick survival. The sources and

timing of mortality are very difficult to determine for precocial shorebird chicks (Nol 1989, Ens et al. 1992). Chicks often leave the nest within a few hours of hatching, after which they are cryptic and highly mobile. Dead chicks are quickly scavenged or washed away by the tide, which further reduces the chance of learning the cause of death. Studies of other shorebird species have identified chick age, mass at hatching, human disturbance, habitat quality, access to foraging sites, rainfall, and an array of predator species as factors affecting chick survival (Dinsmore et al. 2002, Ruhlen et al. 2003, Ruthrauff and McCaffery, 2005, Colwell et al. 2007). Because many breeding attempts fail during the chick-rearing stage, several recent studies have stressed the need for a better understanding of the factors affecting American Oystercatcher chick survival (Davis et al. 2001, McGowan et al. 2005a). In 2004 I initiated a study of American Oystercatcher chick behavior on Cape Hatteras National Seashore. Relatively little was known about how Oystercatcher broods used their habitat and responded to human activity. Anecdotal observations suggested that breeding adult Oystercatchers altered their behavior in the presence of humans and vehicles by hiding their chicks in the dunes and keeping them off the beach. The objectives of this study were to identify patterns of chick behavior and habitat use, quantify the effects of vehicles on Oystercatcher chick behavior, and compare the effects of two management actions (closed beach versus partial beach closures). In 2005, 2006 and 2007 I used radio telemetry to track Oystercatcher chicks on Hatteras Island, Cape Hatteras National Seashore, and North Core Banks, Cape Lookout National Seashore to identify the timing and sources of chick mortality. Here I summarize the results of reproductive success monitoring on the Outer Banks and take an information theoretic approach to examine variation in nest and chick



survival with respect to age, season, year, island, presence of off road vehicles, and habitat quality.

## Methods:

### *Study area*

Cape Lookout and Cape Hatteras National Seashores (Figure 1) comprise over 160 km of barrier island habitat in North Carolina. The islands are characterized by wide barrier beaches with a primary and secondary dune complex broken by flats and overwash fans. The dunes fade into wax myrtle (*Myrica cerifera*) scrub and then to saltmarsh bordering the back bays and sounds. This system is subject to periodic washover events, followed by recolonization by dune grasses. Cape Lookout and Cape Hatteras support approximately 90 breeding pairs of Oystercatchers which nest on the sand flats and dunes and forage along the beach and salt marsh. Off road vehicles are permitted on beach and interdune roads in both parks except in designated wilderness areas or sensitive bird or turtle nesting areas. Cape Hatteras has a permanent road system and several small towns along the length of the islands.

### *Nest survival*

Surveys of breeding Oystercatchers on the Outer Banks began in late March each year. Nests were located by walking or slowly driving along the barrier beach and back-road system. When an adult Oystercatcher was located, observers watched for behavioral cues that indicated the bird had a nest. Although nesting Oystercatchers do not usually employ “broken-wing” distraction displays typical of smaller shorebirds, they do exhibit easily identifiable behaviors such as false incubating and alarm calling. When breeding behavior

was observed, scrapes were found by following the tracks of the adult birds, or by systematic searches. Once located, nests were marked with a small wooden stick placed at least 5m from the nest and concealed to prevent detection by predators, or by using adjacent natural landmarks like driftwood, shells, etc. as a reference. The location of each nest was recorded with a handheld GPS. Nests were checked every 1-4 days until hatching or failure. We made every effort to minimize disturbance and reduce any effect of our observations on nesting success. If a bird was seen incubating, the nest was considered active and was only checked periodically to determine if the chicks had hatched. We avoided walking directly to nest sites, and spent a minimal amount of time in the vicinity of the nest to minimize cues for predators. If a nest failed, we attempted to determine the cause of failure by searching the area for signs of predators, storm overwash, or other sources of nest failure. For example, when a storm event washes out a nest, the nest scrape is usually gone and a debris line is evident above the nest's original location. Unfortunately, such evidence does not last long on a barrier beach, so it was not always possible to determine the causes of nest failure.

I developed a set of hypotheses to explain variation in nest survival on the Outer Banks from 1999 to 2008. The hypotheses described below were incorporated into candidate models as covariates.

- 1) *Year.* Year to year variation in weather patterns, timing of storms, prey abundance, predator abundance, and numerous other factors that were not explicitly measured could affect Oystercatcher nest survival
- 2) *Island.* The study area is composed of six islands in two national parks. Human use of the seashores varies considerably from island to island,

along with predator composition and abundance. Differences in these and other factors could explain variations in nest survival.

3) *Presence of Off Road Vehicles.* Vehicle activity can affect nesting behavior (McGowan and Simons 2006) and nest survival for beach nesting birds (Buick and Paton, 1989, Novick 1996, Davis 1999, Carney and Sydeman 1999). Although many of the nests in the study area were protected from direct impact by signs and symbolic fencing, I hypothesized that the indirect effects of adjacent vehicle traffic would lower survival for nests on beaches open to vehicles. I considered a beach open for vehicle traffic if vehicles were allowed to pass above or below the nest, even if the nest itself was in a closed area. I did not attempt to include distance from nests to vehicles or the number of vehicles using the beach, as these data were unavailable for most of the nests.

4) *Distance to the high tide line.* Oystercatchers nest anywhere from within a few meters of the high tide line to hundreds of meters away on large sand flats. Overwash from storms and spring tides is a major source of nest failure. In addition, the majority of vehicle traffic is located near the high tide line. I hypothesized that nest survival would increase with distance from the high tide line.

5) *Direct access to foraging habitat.* Oystercatchers will forage on the ocean beach, but most birds maintain primary foraging territories in the creeks and mudflats on the back side of the barrier islands. If a nesting oystercatcher

has to fly a long way to get to their foraging site they are unavailable to help their mate defend the nest from predators. Perhaps more importantly, nest sites adjacent to foraging territories may be very important during chick rearing (Ens et al. 1992, Heg and van der Velde 2001, Kersten and Brenninkmeijer 1995, van de Pol 2007). Older, more experienced birds are likely to occupy these prime territories, so this covariate may be an indirect measure of adult quality. I hypothesized that direct access to primary foraging habitat would increase nest survival.

6) *Time of the nesting season.* The nesting season on the Outer Banks of North Carolina spans approximately five months. I fit linear and quadratic time trend models to the null model of constant survival to evaluate temporal variation in nest survival within the nesting season. For the linear model I predicted that survival would decrease through the season. The quadratic model allowed for a non-linear change in nest survival to account for more than one survival peak or valley.

#### *Brood and chick survival*

When a nest hatched, the young were observed every 1-4 days until fledging, or until all the chicks died or disappeared. I documented habitat use and behavior of Oystercatcher broods on Cape Hatteras National Seashore from 2004 to 2007 using behavioral observations. I did not have the option of experimentally manipulating the disturbance level or closed/open status of the beach (e.g. Simons and Tarr 2008), so this was strictly an observational study. We conducted observations in hour-long intervals, taking instantaneous

habitat information at two minute intervals. Broods were observed through scopes from a distance where observer presence did not affect the bird's behavior. Habitats were designated as; below the tide line, open beach, and dunes or grass. Watches continued if the birds went out of sight as long as we could still determine the habitat type. This prevented a negative bias for dune and grass habitats where the birds are less visible. We observed chicks of all ages from hatching through fledging at all times of day and stages of the tide. We were not able to conduct behavior watches at night, but I did periodically check on the location of broods at night to document habitat use. Observation windows were randomly assigned to active Oystercatcher broods throughout the nesting season.

With careful monitoring it was possible to determine annual productivity, or the number of chicks fledged per pair, per year, although usually not the cause or exact timing of chick mortality. Adult Oystercatchers exhibit markedly different behavior patterns when they have chicks. They are much more aggressive toward intruders, and give distinct alarms calls. We determined whether a pair of adult birds had chicks by observing adult behavior, even if we could not locate the chicks. In most cases chicks were located by observing adults from a distance using a spotting scope, and occasionally a portable blind. When we found dead chicks or observed predation events we recorded the cause of death.

In addition to an analysis of brood survival, I examined factors affecting individual chick survival and sources of mortality for a subset of chicks using radio telemetry. From 2005 to 2007 I radio tagged a total of 121 chicks on Hatteras Island, Cape Hatteras National Seashore, and North Core Banks, Cape Lookout National Seashore. Chicks were radio tagged as soon as they were mobile, usually within 24-48 hours of hatching. I attached ATS

A2420 transmitters (1.3 grams) to the scapular region of the chick using surgical grade skin glue (Figure 2). Chicks were checked every 24 hours for the first week, and every 1-3 days thereafter. Transmitter range was 400-1000 meters depending on terrain. When a chick died, I tried to locate the remains and determine the cause of death. In 2005 and 2006 I exchanged the ATS transmitters for larger PD2 model transmitters from Holohil Systems when the chicks reached four weeks of age. These transmitters were designed to last at least six months and were attached to a permanent leg band (Figure 2).

### *Statistical analysis*

Previous analyses compared estimates of apparent nesting success using the binomial proportion of successful nests to failed nests, with Mayfield nest survival estimates (Mayfield 1961, 1975, Davis, 1999, McGowan 2004). As expected, these results showed that apparent nest success overestimated survival because of nests that failed and were never found. I analyzed our nest survival database from the period 1999-2008 using the nest survival module in Program Mark (White and Burnham 1999, Dinsmore et al., 2002). This method is similar to the Mayfield method in that a daily survival rate is calculated from nest observation days and thus accounts for missed nests. Daily nest survival is defined as the probability of surviving from day  $i$  to  $i + 1$ . Program Mark uses a maximum likelihood method to estimate the nest failure date when the time between nest checks is greater than 1 day, and it allows for modeling covariates to explain variations in nest success and the comparison of alternative models using Akaike's Information Criteria (AIC) (Akaike 1973, Burnham and Anderson 2002).

Based on our hypotheses and predictions described above, I evaluated seven

covariates; Linear time trend, quadratic time trend, year, island, foraging access, distance to the tide line, and presence of off road vehicles. Foraging access was a binary individual covariate based on access to foraging sites for nesting pairs. The covariate was positive if a pair had direct walking access to a primary foraging site. Primary foraging sites were defined as mudflats, saltmarsh creeks, tide pools and intertidal oyster beds. The individual covariate “distance to high tide line” was measured by calculating the distance between nest locations and recorded high tide lines in ArcMap (Esri 2009). Presence of off road vehicles was recorded for each nest based on beach closure records from the National Park Service. Off road vehicles were considered to be present if any part of the beach above or below the nest was open to vehicle traffic, regardless of whether the nest itself was in a vehicle enclosure. I did not account for differences in traffic volume or enclosure size, as these data were not available for the majority of our nests. I used a three-step hierarchical process to evaluate different models. In the first step I created models with linear and quadratic time trends as well as a null model of constant survival. I then added effects of year and island to the best model(s) ( $\Delta AICc \sim < 2.0$ ). Finally I added the covariates for tide distance, foraging, and ORV access to the new best model(s).

In our analysis of factors affecting chicks during the pre-fledging period, I considered chick survival and brood survival separately. Chick survival was defined as the probability of a single chick surviving from hatch to fledging, while brood survival was defined as the probability of at least one chick in a brood surviving to fledging. Because of the difficulty in determining the status of individual chicks during each monitoring check, I developed hypotheses and analyzed covariates associated with brood survival, rather than individual

chick survival. I developed models incorporating these hypotheses using the nest survival module in Program Mark. Our hypotheses about factors affecting brood survival were similar to nest survival. I did not include an effect of distance to high tide because Oystercatcher chicks are highly mobile. I also examined the effect of brood age on survival, hypothesizing that daily survival would increase with brood age. Covariates included in the brood survival models were year, island, presence of Off Road Vehicles, direct access to foraging habitat, time of the nesting season (linear and quadratic trends), and age of the brood (linear and quadratic trends).

I used a multi-step approach to model construction, similar to the nest survival analysis. In the first step I ran models with linear and quadratic time and brood age trends as well as a simple null model of constant survival. I then added the effects of year and island to the best model(s). Finally I added the covariates for presence of off road vehicles and foraging access to the best model (inclusive of year and/or island effects) to see if they contributed any useful information to the best model.

In addition to modeling nest and brood survival, I used t-tests to compare habitat use on beaches open and closed to vehicles. I estimated survival probability for radio tagged chicks using the Kaplan-Meier known fate procedure (Kaplan and Meier 1958). Day zero was defined as the day of hatch regardless of capture date. Multiple chicks from the same brood were tagged and followed, which violates the assumption of independent observations. The result is that the survival estimator was unbiased, but the standard error was likely underestimated (Pollock et al. 1989). Values reported in the Results section are means  $\pm$  SE.



## Results:

### *Nest survival*

This analysis is based on a sample of 1172 nests monitored on six islands from 1999-2008 where sufficient data were collected for nest survival analysis. Nests were monitored during a 126-day window (April 2 to August 6) during the 10-year period for a total of 15736 exposure days. Overall observed hatching success from the beginning of egg laying to hatching for all years and locations was 0.280 (0.013). The single estimate of daily survival from Program Mark (null model) was 0.950 (0.002). The average incubation period for Oystercatcher nests is 27 days (Nol and Humphrey 1994). To obtain the probability of nest survival to hatching (period nest survival) I raised estimates of daily survival rates (DSR) to the 27<sup>th</sup> power. Period survival for the null model was  $0.950^{27} = 0.250$  (0.011).

Variation in nest survival was best explained by a model with a linear within-season time trend and additive covariates for year and island (Table 1). The quadratic time effect was not supported (~ one unit increase in AICc, for a one parameter increase, lower model weights, and 95% CI for the beta coefficient overlapping zero). A linear time effect was supported in all the top models, indicating that nest survival declined over the nesting season (B = -0.005, CL = -0.008, -0.001). The 95% confidence intervals for the beta coefficients of five of the ten years (2000, 2001, 2003, 2007, and 2008) overlapped zero, indicating no significant difference in survival from the baseline year (1999). In contrast, the entire confidence interval for the coefficient for 2002 was below zero, while the intervals for 2004, 2005 and 2006 were all above zero. 2004 had the highest beta coefficient of any year (B = 0.882, CL = 0.522, 1.241). Nests on the island of South Core Banks had lower overall

survival ( $B = -0.327$ ,  $CL = -0.499, -0.156$ ) than North Core Banks, while Ocracoke ( $B = 0.407$ ,  $CL = 0.136, 0.677$ ) and Hatteras ( $B = 0.323$ ,  $CL = 0.107, 0.538$ ) were higher than North Core Banks over the course of the study. The 95% confidence intervals for the beta coefficients of Middle Core Banks and Bodie Island overlapped zero, indicating no significant difference in survival from North Core Banks.

One of the top two models by AICc rank included a covariate for ORV presence. In this model nests with ORV access had a lower survival rate, but support for the ORV covariate was weak as the 95% confidence interval for the beta included zero ( $B = -0.196$ ,  $95\% CL = -0.472, 0.080$ ) and there was no change in AICc. Models that included covariates for access to foraging habitat, and distance to tide line also received some support ( $\Delta AICc < 2$ ), but the confidence interval of the beta coefficient for each of the covariates also included zero.

Mammalian depredation was the major identifiable cause of nest failure at our study sites, accounting for approximately 54% of identified nest failures (Figure 3). Over-wash and other weather related causes accounted for 29% of identified failures. The remaining identified failures (17%) were caused by human activity, avian predators, ghost crabs, or unknown reasons (Figure 3). Human activity was defined as a human action directly leading to nest failure, such as physical destruction of the eggs, and did not include indirect effects of disturbance. I could not identify the causes of failure for 52% of failed nests. The sources of nest mortality were similar on Cape Hatteras and Cape Lookout, but the relative proportion of nests lost to each source varied by year and location (Figures 4 and 5),

Clutch size averaged 2.35 (0.01) eggs per nesting attempt. A nesting attempt was

defined as a nest with at least one egg. Pre-nesting scrapes were not considered nesting attempts. When a nest failed, Oystercatcher pairs waited 9-14 days before initiating a new clutch. If a nest hatched successfully pairs did not re-nest unless the chicks were lost while still very young (<7 days). Oystercatcher pairs initiated between one and five nests per season with an average of 1.55 (0.01). The average number of clutches per pair ( $y$ ) was logarithmically related to overall nest survival ( $x$ ) ( $y = -0.375\ln(x) + 1.0873$ , Figure 6).

#### *Brood and chick survival*

Our analysis of factors affecting brood survival is based on a sample of 306 broods on Cape Lookout and Cape Hatteras National Seashores from 1999 to 2008. Mean brood size at hatch was 1.99 chicks (0.042), while the mean daily brood survival was 0.981 (0.002). Mean period survival for the 40 day pre-fledging period was 0.471 (0.030).

Our best model of factors affecting brood survival included covariates for the age of the brood, island, presence of off road vehicles, and access to foraging habitat. This model was the only supported model in our set (model weight = 0.991,  $\Delta$ AIC of next model = 9.443). Within-season time trends and year effects were not useful in explaining variability in brood survival rates. The best model included a quadratic term for brood age (Table 2), with daily survival rates increasing rapidly for the first two weeks, and then leveling off (Figures 8 and 9). Brood survival varied between islands. Survival was highest on Middle Core Banks, Cape Lookout National Seashore ( $B = 0.722$ ,  $CL = -0.379$ ,  $1.823$ ) and lowest on Bodie Island, Cape Hatteras National Seashore ( $B = -0.72597$ ,  $CL = -1.819$ ,  $0.367$ ). The within-island variability in survival was very high however, and only South Core Banks had a beta coefficient with a confidence interval that did not include zero ( $B = -0.688$ ,  $CL = -0.213$ , -

0.164). Predicted brood survival was lower when off road vehicles were present (Figure 7,  $B = -0.991$ ,  $CL = -1.381, -0.601$ ) and higher when broods had direct access to foraging areas (Figure 8,  $B = 0.717$ ,  $CL = 0.277, 1.156$ ).

Individual chick survival and sources of chick mortality were determined from the radio telemetry study. One hundred and twenty-one chicks were tracked from hatching to fledging or death. I was able to determine the cause of death for 37 chicks. Predators accounted for 54% ( $N = 21$ ) of chick loss and included Great Horned Owls (*Bubo virginianus*), Fish Crows (*Corvus ossifragus*), Feral Cats (*Felis catus*), Raccoons, (*Procyon lotor*), American Mink (*Mustela vison*), and Ghost Crabs (*Ocypode quadrata*) (Figure 9). Vehicle traffic was directly responsible for 16% ( $N = 6$ ) of chick deaths. Environmental factors, including starvation and storm events claimed 30% ( $N = 10$ ). I was unable to determine the cause of death for 51% ( $N = 39$ ) of the mortality events. Dead chicks were quickly carried off by predators and scavengers or washed away by the tide, so even with transmitters I could not always find and retrieve dead chicks. Highest chick mortality rates occurred in the first week after hatching, and during the week of fledging (Figure 10). The cumulative probability of surviving the pre-fledging period varied with the definition of “fledged”. Thirty-five days is the minimum age I observed chicks achieving sustained flight (>100m). Survival to 35 days was estimated at 0.438 (0.0459). A few chicks took up to 46 days to fledge, however, which reduced the survival probability to 0.280 (0.168). The wide confidence interval after 40 days is a result of very few chicks in the sample still alive and unfledged at this age.

After fledging, radio-marked chicks were tracked daily until mid-August, when field personnel were no longer available. No fledgling mortality was documented during this time. Survey flights in late August and early September in 2005 and 2006 covered the Outer Banks from Nags Head to Morehead City. The oldest chicks began to migrate out of the study area by the end of August, but several still remained at their natal sites on the last survey flight on September 18 2005 and September 25 2006.

I conducted 169 hours of behavioral observation on 63 chicks on Cape Hatteras National Seashore over four years (2004-2007). Over 90% of the observations were of chicks in full-beach closures because most of the locations where chicks hatched were subsequently closed under Park Service policy. Chicks on beaches where vehicles were present spent significantly more time hiding in the dunes and less time at or below the high tide line than chicks on beaches closed to vehicles. (Figure 11,  $t = 2.00$ ,  $p = 0.047$ ). Chicks on beaches open to vehicles often ran back and forth from the beach to the dunes in response to vehicles, humans and dogs. Oystercatchers with chicks showed a stronger reaction to humans with dogs than to humans alone. I did not document any dog-related mortality, but dogs were observed chasing adult Oystercatchers on several occasions. Most adults began to bring their chicks to the waterline to forage within 24 hours of hatching. Broods ranged up and down the beach from their nest sites, often moving 500 meters or more each day. This pattern continued throughout the chick-rearing stage. Night observations of chicks invariably found the broods on the open beach or below the tide line on both open and closed sections of beach. During the day chicks spent most of their time hiding in the dunes, particularly in areas open to vehicles. Parents always brought their chicks to the beach around sunset. I

observed Oystercatchers of all ages that became disoriented by vehicle headlights at night and walked, ran, or flew toward the light source. I also observed adult Oystercatchers who were startled and apparently disoriented by headlights and abandoned their chicks until the vehicles had passed. In some cases adults returned quickly to their chicks, but in at least one case the adults were kept away by multiple vehicles passing, which resulted in the deaths of their young chicks, from exposure and depredation by Ghost Crabs.

I estimated total productivity as the number of chicks fledged per nesting pair, from 1036 pairs and 1581 clutches monitored between 1995 and 2008. Productivity was highly variable among years and among locations (Appendix A). A total of 320 chicks fledged from all study sites between 1995 and 2008. On average, 0.309 (0.020) chicks fledged per nesting pair. Total productivity (P) is defined as the number of fledged chicks per nesting pair (pair that laid at least one egg). Productivity is a function of nest survival ( $S_N$ ), chick survival ( $S_C$ ), chicks hatched per successful nest ( $H_C$ ), and total nests per breeding pair. As we have seen, the number of nests per pair is a function of nest survival (Figure 6), so the equation for productivity can be written as:

$$\text{Equation 1: } S_N * S_C * H_C * (-0.04139(\text{LN } S_N) + 1.1099) = P$$

This equation is useful because it allows us to separate the components of overall productivity and therefore to predict the effect of a change at each stage of the nesting season.

## Discussion:

The factors affecting American Oystercatcher reproductive success on the Outer Banks of North Carolina differed for the incubation and chick-rearing stages. This is not particularly surprising given the semi-precocial nature of oystercatcher chicks. One would expect different sources of mortality after the chicks leave the nest and begin to move about their environment. It is instructive from both an ecological and a management standpoint to examine where the differences occur and how different factors influence overall reproductive success. Nest survival through the incubation period was primarily influenced by the date of nest initiation, the nesting island, and year to year variation in nesting conditions. Nest survival showed a linear decline over the nesting season. There was little support for a quadratic model where the rate of change in nest survival could vary across the season. Numerous studies have found trends in daily survival rates when they relax the common assumption of constant survival over the season or the age of the nests (Ainley and Schlatter 1972, Klett and Johnson 1982, Dinsmore et al. 2002). The decline in nest survival over the season could be the result of multiple factors. Heat stress, human activity, and predator abundance and distribution may all change over the course of the season. Predators were directly responsible for the majority of failures (61%) where the source of nest loss could be determined. Differences in nest survival among islands and years may largely be a result of differences in the suite of nest predators and changes in predator abundance. In the absence of comprehensive data on predator populations this explanation is hypothetical, but there is some evidence to support the idea. On Hatteras Island, Cape Hatteras National Seashore, the nest survival rate fell from 0.272 (0.048) in the period 1999–2001 to 0.030 (0.023) in 2002,

after foxes colonized the island. Predator control measures were initiated in 2003 and the nest survival rate increased to 0.506 (0.050) from 2003-2008. On North Core Banks, Cape Lookout National Seashore, the proportion of nests positively identified as lost to predators dropped from 0.31 to 0.10 after Hurricane Isabel flooded the island in September 2003 and apparently reduced predator populations (Schulte and Simons in review).

Given the importance of depredation as a source of nest failure, human actions that affect predator populations or the ability of predators to locate nests will have the greatest effect on nest survival. McGowan and Simons (2006) found that oystercatcher nests that were frequently disturbed were more likely to be depredated. Frequent disturbance may make the nest more visible to avian predators and increase the number of scent trails leading to the nest. I hypothesized that nests on beaches open to vehicle traffic would have a lower survival rate as oystercatchers often move away from their nests in response to vehicle traffic. I considered a beach to be open to vehicle traffic if any part of the shoreline was open, even if the upper beach was closed off with symbolic fencing. One of our top two models indicated support for this hypothesis, showing a negative correlation between the presence of off road vehicles and nest survival. This covariate had a large amount of variability and the 95% confidence interval of the beta coefficient just included zero. Much of this variability likely stems from differences in physical conditions, human activity, and oystercatcher behavior across the islands of the Outer Banks. The effect of vehicle traffic on nest survival could be quite different for a nest on a low-traffic, wider beach and a high-traffic narrow beach. Oystercatcher behavioral responses may also vary from pair to pair, with some birds habituating to human activity and others becoming more sensitized. Finally, the linkage



between disturbance and nest failure should vary with the local predator population. The negative effect of disturbance should be greater in areas with higher predator populations. Our beach closure status covariate is not sensitive to these potentially interacting factors, but it does provide a general measure of the correlation between the presence of vehicles and nest survival. An experimental approach that manipulated disturbance levels and controlled for other factors could effectively reduce the uncertainty in this relationship. Tarr et al (2010) used this approach to evaluate the effect of vehicle disturbance on shorebird roosting and foraging behavior during fall migration on Cape Lookout National Seashore.

Storms and high tides are another source of nest failure. Breeding season storms can result in significant nest loss as nests are flooded out or sanded over. A strong storm at the wrong time of year can eliminate most of the active nests, which sets back the reproductive cycle by 2-6 weeks. Hurricanes and strong winter storms do not directly affect nest success because they usually occur outside of the breeding season. These storms can have beneficial effects as they create new nesting habitat and may reduce predators. I predicted that nest survival would increase with distance from the high tide line. This hypothesis was not supported by our data. Models with the tide covariate received less support than the same models without the covariate and the confidence interval of the beta coefficient for the tide covariate encompassed zero. Height above high tide may be a better predictor of success, as some nests on low-lying flats may be hundreds of meters from the high tide line but still flood during storms. Unfortunately, measurements of height above high tide were not available for our nests.

Proximity to foraging area was another factor I considered. I predicted that pairs with

adjacent foraging habitat other than the ocean beach would have higher nest survival. Birds with nearby foraging habitat should spend less energy on flight, and both adults would be present to defend the nest and territory as needed. I did not include the ocean beach in this analysis because it is typically not the primary foraging habitat and almost every pair had access to the beach. In addition, oystercatcher pairs that are able to maintain territories near high-quality food resources may be older, more experienced birds. European oystercatchers may wait years for the chance to establish a territory in high-quality habitat adjacent to feeding areas (Ens et al 1995, Heg and van der Velde 2001, van de Pol 2007). In our study I found no effect of forage proximity on nest survival.

I was not able to observe the causes of most nest failures directly so I relied on indirect evidence, such as eggshell fragments, or predator tracks, to infer the causes of nest failures. Nests reported as undetermined generally represent nests where wind or rain erased any clues of the causes of failure. I believe that the vast majority of our unidentified failures are a result of nest predators. Storm losses were usually easy to identify as the tide line following the storm was often evident above the level of the nest, or the nests were completely sanded over. Identification of different nest predators was much more difficult. Avian predators can leave little or no sign at the nest, and the tracks of mammals such as raccoons and cats are quickly blown away. Even during calm weather, predator tracks were often obscured by Oystercatcher tracks as the pair returned and walked around the nest scrape after a predation event. The difficulty of identifying different sources of failure suggests that storm losses may be over-represented in our estimates of identified nest failures (Figure 3). It is also possible that avian predators are under-represented in these estimates

because these predators often leave little evidence. Losses from avian predators usually result in clutch reductions as often only a single egg is taken. Most nest failures occur overnight with the loss of an entire clutch of eggs, suggesting mammalian depredation.

Oystercatcher brood survival did not change with the date of the nesting season, but survival was affected by the age of the brood. Most brood losses occurred in the first week to ten days after hatching. This pattern resembles that of other species with precocial young (Colwell et al. 2007, Ruthrauff and McCaffery 2005). Young chicks are mobile but cannot fully thermo-regulate and are more susceptible to temperature and weather extremes. Smaller chicks are also vulnerable to a wider range of predators. Parental behavior may draw attention to younger chicks that have to be brooded more often and thus stay close to one of the parents. This is particularly true for oystercatcher chicks as they are the one of the only shorebird chicks that are fully dependant on their parents for food (Nol and Humphrey 1994). The Oystercatcher's ability to bring food to their young allows them to exploit nesting sites without local food resources. Broods raised at these sites should be expected to have generally lower survival because parents must bring food from a separate foraging territory. A long-term study of breeding Eurasian Oystercatchers found that pairs with walking access to foraging habitat had significantly higher productivity than pairs that had to fly to their foraging territories (Ens et al. 1992). Our best model predicted lower survival for broods without direct access to foraging habitat (figure 7), which is consistent with our a priori hypothesis.

Brood survival was directly and indirectly affected by the presence of off road vehicles. Broods on beaches open to vehicles survived at a lower rate than broods on closed

beaches (Figure 7). Radio tracking Oystercatcher chicks provided insights into possible mechanisms shaping this pattern. Prior to this study, very little was known about factors affecting chick survival. Identifying sources of chick mortality without radio telemetry is extremely difficult. Oystercatcher chicks are well camouflaged and even live chicks are hard to locate. Chicks that die below the high tide line are washed away and predators and scavengers quickly claim the rest. From 1995 to 2008 (excepting the birds in the telemetry study) 395 Oystercatcher chick deaths were recorded on Cape Hatteras and Cape Lookout. Only 25 dead chicks were found during this period (6.3%). Of these 25 chicks, 13 (54%) were killed by vehicles. Through the use of radio transmitters I was able to closely track chick movements and located 50% of the chicks that died. I found that very young chicks are highly mobile, much more so than previously believed. Movement between the dunes and the intertidal zone places young chicks at considerable risk from beach traffic. I regularly observed chicks hiding in vehicle tracks in response to adult alarm calls and also observed chicks, and even some adults, running or flying directly at the headlights of oncoming vehicles at night. Shortly after I initiated the radio tracking study, I documented the loss of a brood of two-day old chicks to a vehicle on Cape Lookout National Seashore. I radio-tagged the recently hatched brood at the nest on June 16 2005. That same evening the chicks were relocated hiding in seaweed at the tide line with the adult pair. The following morning I tracked the transmitter signals to a nearby location and found two of the chicks crushed in a fresh all terrain vehicle tire track, just above the high tide line (Figure 12). Over the course of the three-year telemetry study I identified the cause of death for 37 chicks, of which six (16%) were vehicle-related. After reviewing the data on sources of chick mortality, Cape

Lookout National Seashore initiated a policy under which they closed sections of beach with unfledged chicks to vehicle traffic, and re-routed traffic around the birds via a back road. After the beach sections were closed, chicks were regularly observed on the open beach and at the tide line during daylight hours, suggesting that vehicle traffic was altering chick behavior and foraging patterns.

I found that disturbance by vehicles during the chick-rearing phase produces measurable differences in Oystercatcher chick behavior, habitat use, and survival. In addition to being at risk from direct mortality from vehicles, chicks in partial closures spent 74% (44.6 min/hr, SE 7.78min) of their time hiding in dunes and vegetation and did not use the intertidal zone. Chicks on closed beaches spent 43% (25.8 min/hr, SE 3.64min) of their time in the dunes and 20% (12.0 min/hr, SE 3.64min) in the intertidal zone (Figure 11). Reduced access to the cooler sand of the intertidal zone may subject chicks to greater heat stress, limit feeding opportunities, and expose them to greater risk from predators such as cats, mink, and raccoons. The increased risk from nocturnal predators probably explains why adults move their chicks from the dunes to the beach every night even if vehicles are present.

Radio tracking individual chicks allowed us to identify a suite of predators responsible for mortality of chicks prior to fledging. Although Feral cats and Raccoons both preyed on chicks, Ghost Crabs and avian predators such as Great Horned Owls and Fish Crows, appeared to play a larger role in chick depredation than nest depredation. The Kaplein-Meier survival curve for radio-tagged chicks showed that chicks were most vulnerable during the first week after hatching when they are most susceptible to exposure

and ghost crab depredation (Figure 10). This result is consistent with the predicted age-related brood survival curve from our best model (Table 2, Figures 7 and 8).

Total nesting productivity, or the number of chicks fledged per breeding pair, reflects the ability of an Oystercatcher population to navigate the hazards associated with reproduction from egg-laying through fledging. Predators, storms, habitat quality, and management actions combine to shape the annual success or failure of each breeding pair. Management actions that affect chick survival will generally have the greatest effect on overall productivity. In 2008 Cape Hatteras National Seashore increased predator trapping efforts and expanded buffer zones for chicks to 300 meters. Chick survival on Cape Hatteras in 2008 was the highest recorded during the study period (0.81), which resulted in a final productivity of 0.714, over twice as high as the average annual productivity in North Carolina. The extent to which predator management versus vehicle management contributed to this elevated productivity is not clear. Given the importance of predators at all stages of the breeding cycle, a better understanding of predator population dynamics would likely go a long way toward explaining temporal and spatial variability in Oystercatcher productivity.

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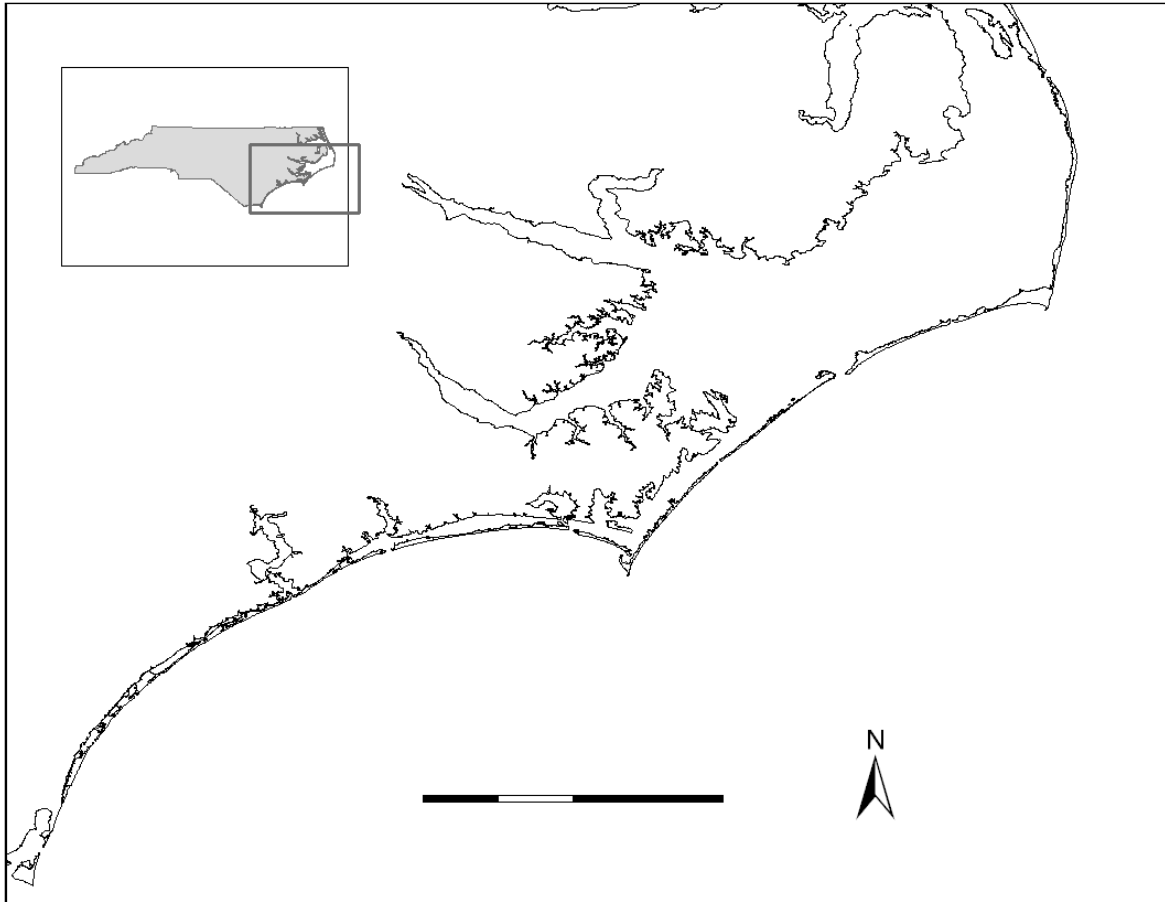


Figure 1.1 American Oystercatcher study sites in North Carolina.



Figure 2.1 Radio tagged American Oystercatcher chicks. Recently hatched American Oystercatcher chicks with glue-on transmitter (right) and post-fledging immature with leg-band transmitter (left).

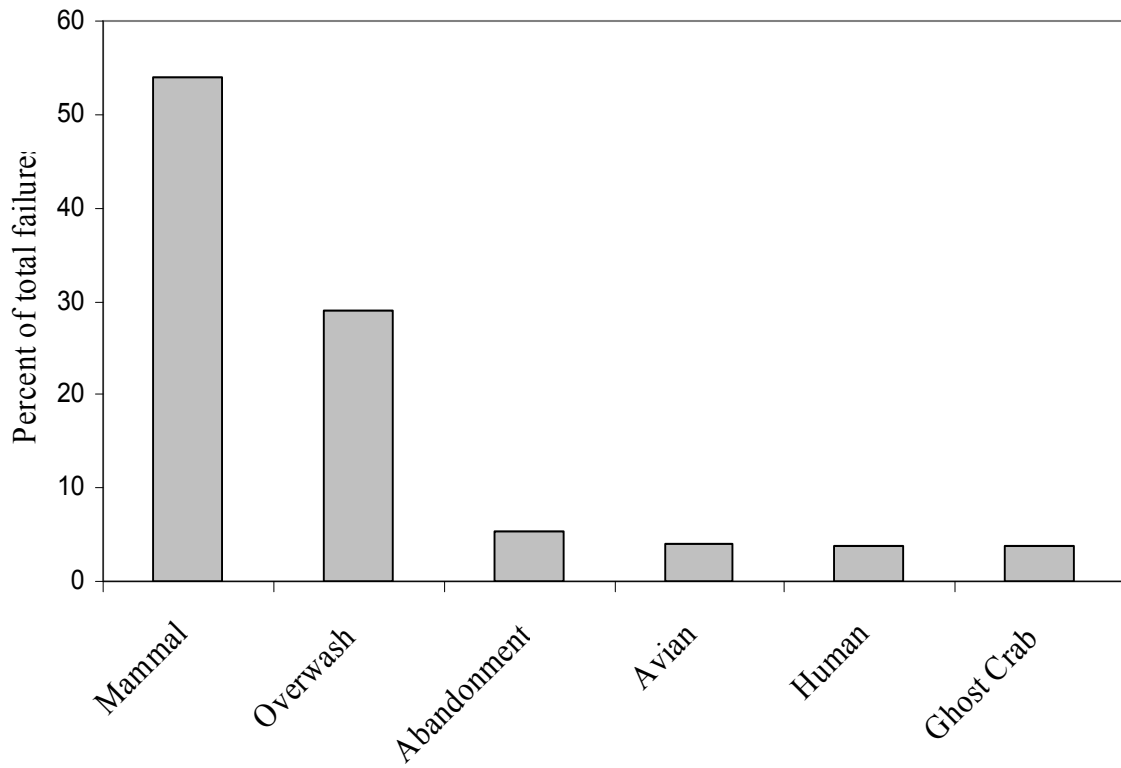


Figure 3.1 Sources of American Oystercatcher nest failure on the Outer Banks of North Carolina from 1998-2008 where cause of failure could be determined (N=481). Cause of failure could not be determined for 49% of nest failures (N=464).

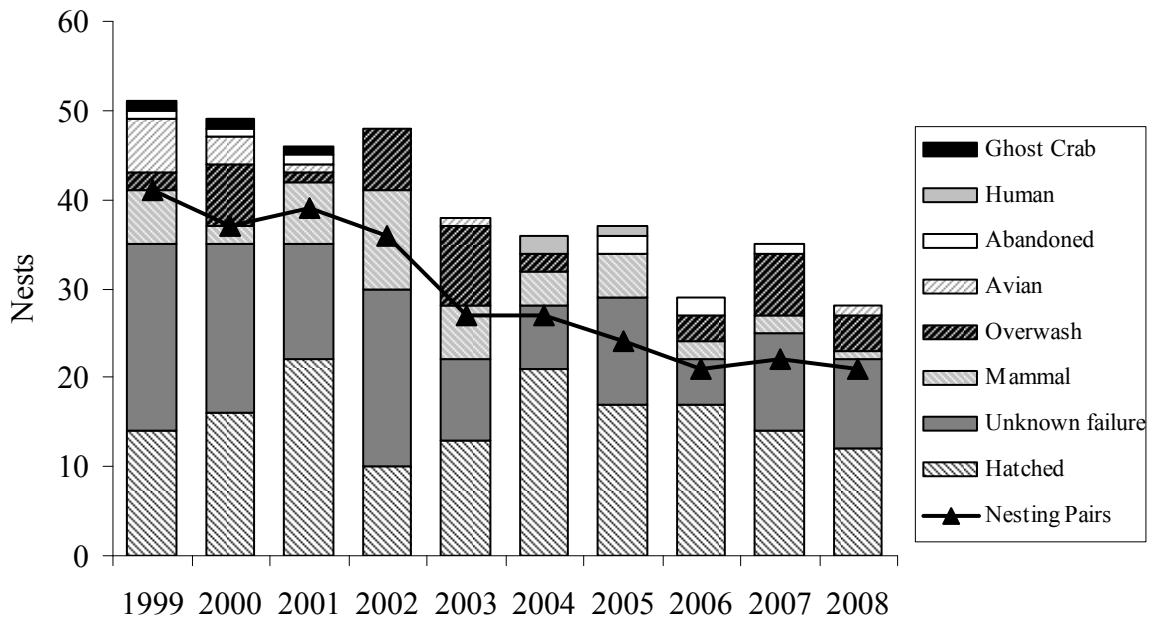


Figure 4.1. Nest fates for American Oystercatcher nests on Cape Hatteras National Seashore from 1999 to 2008. Column segments represent the number of nests in each outcome category.

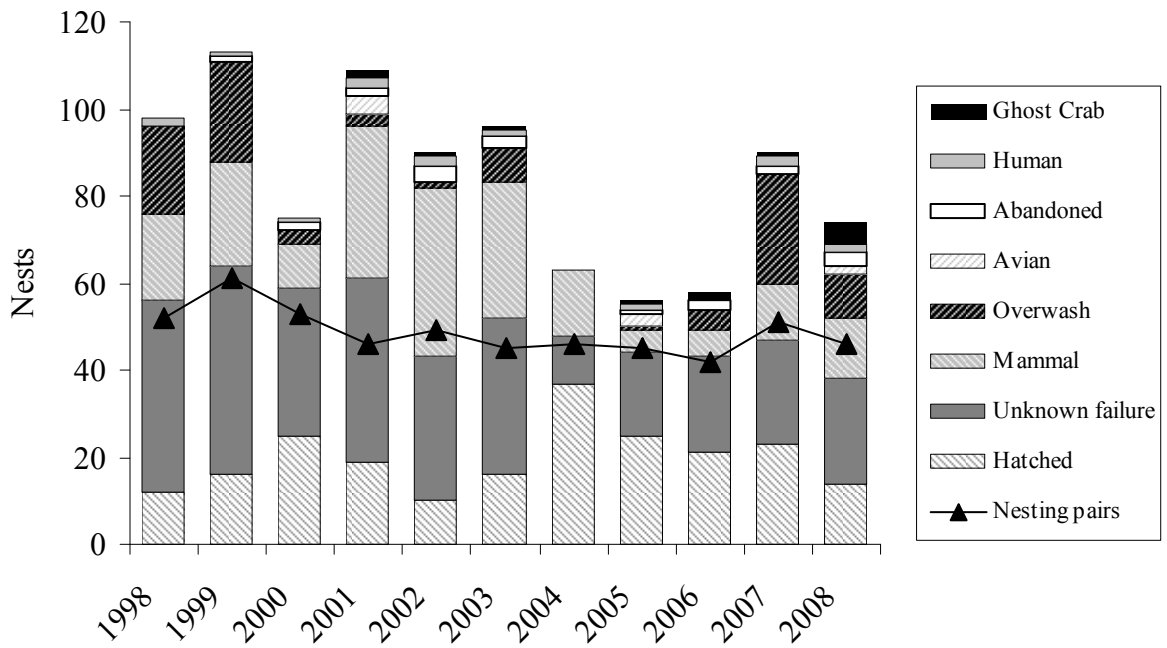


Figure 5.1 Nest fates for American Oystercatcher nests on Cape Lookout National Seashore from 1998 to 2008. Column segments represent the number of nests in each outcome category.



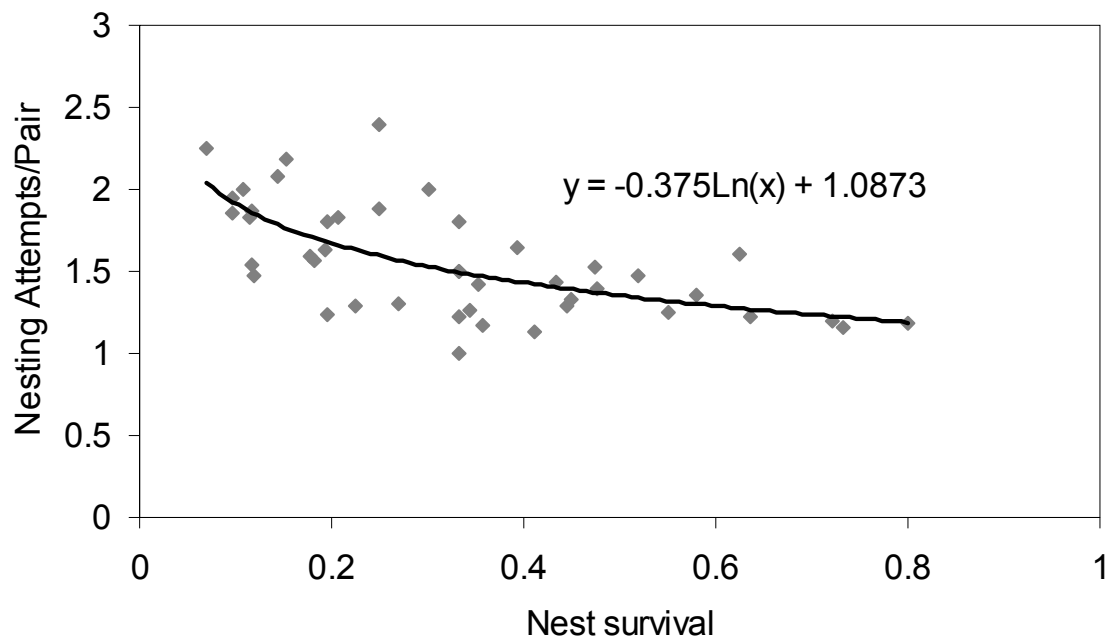


Figure 6.1 The number of nesting attempts per pair as a function of nest survival on Cape Lookout and Cape Hatteras National Seashores. 1998-2008. N=44 location/years, 1234 nesting attempts.

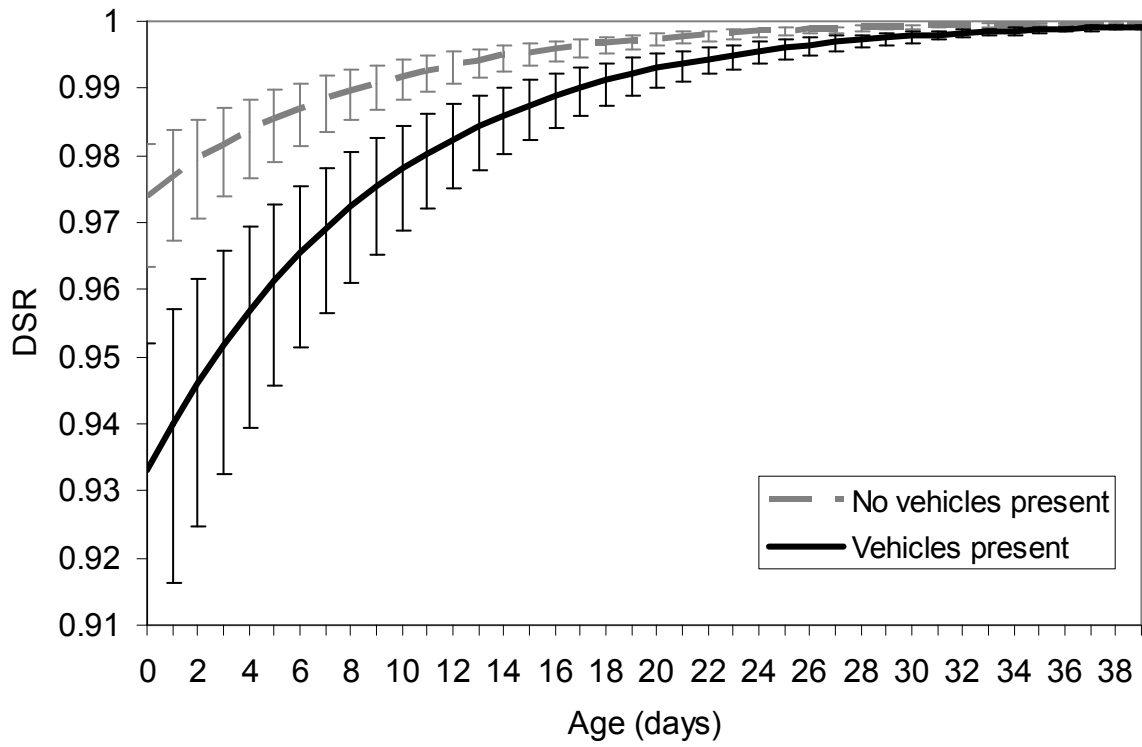


Figure 7.1 Survival curves for American Oystercatcher broods on beaches with and without off road vehicles. Daily survival rates and confidence intervals were estimated from the model with the lowest  $\Delta AICc$  score (Table 2).

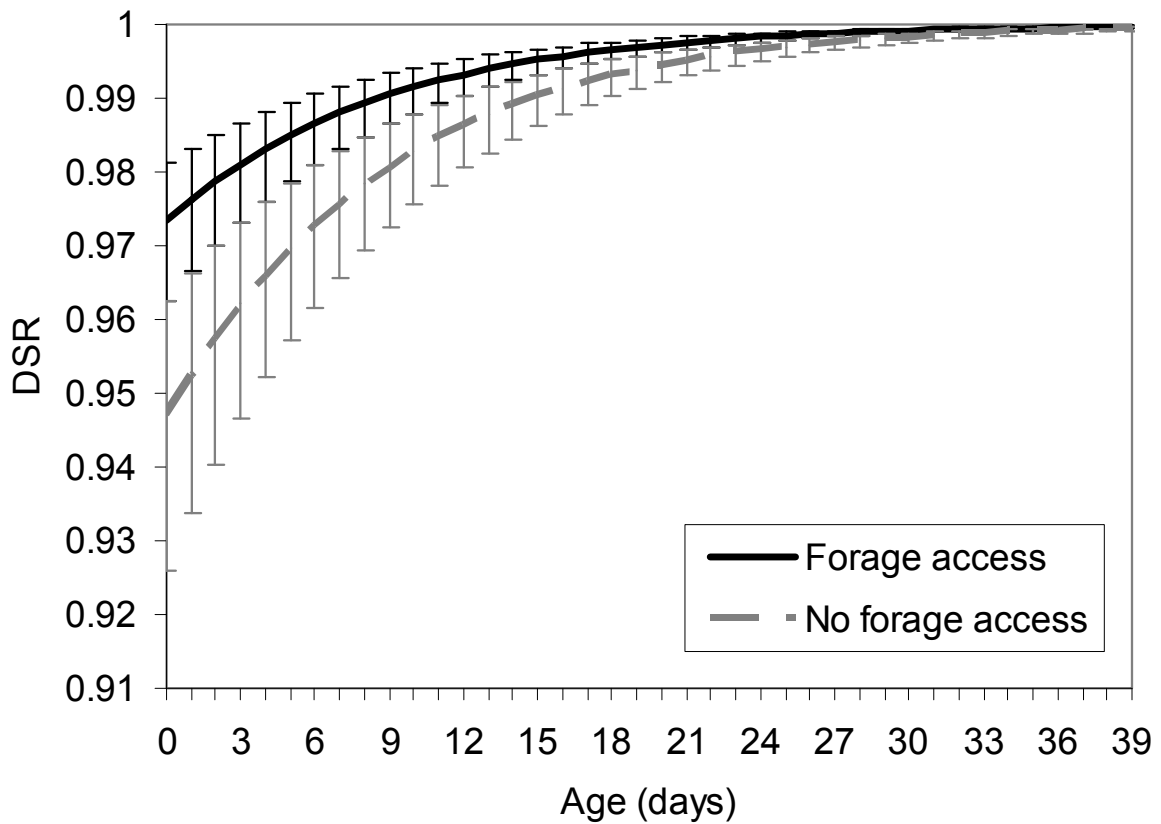


Figure 8.1 Survival curves for American Oystercatcher broods with and without direct access to foraging sites. Daily survival rates and 95% confidence intervals were estimated from the model with the lowest  $\Delta AICc$  score (Table 2).

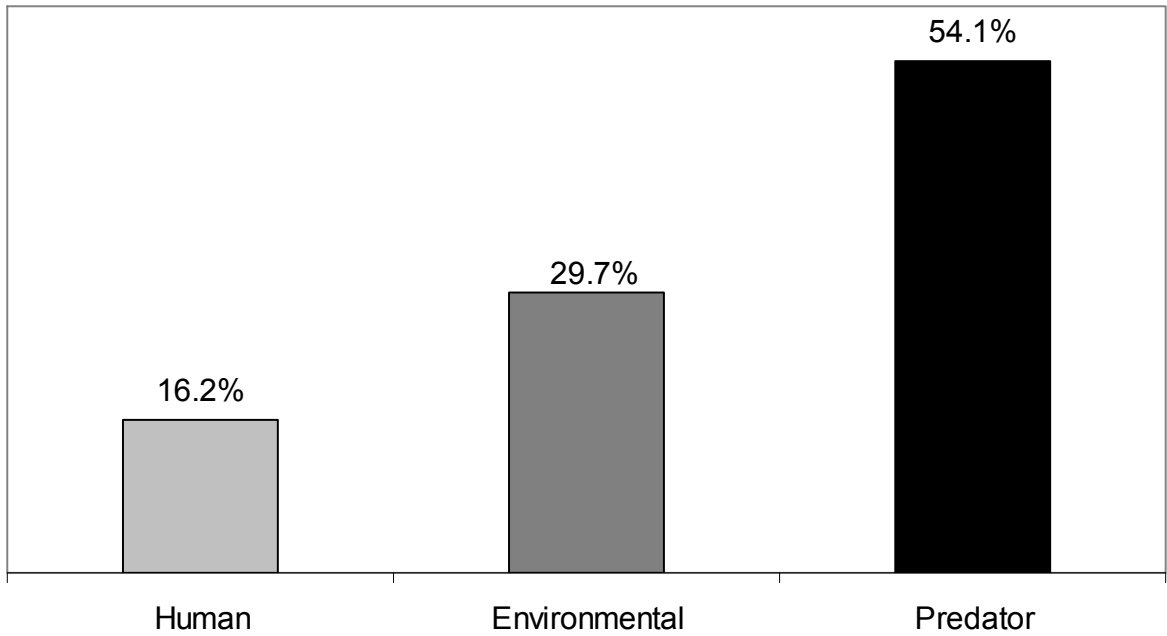


Figure 9.1 Sources of pre-fledging American Oystercatcher chick mortality at Cape Hatteras and Cape Lookout National Seashores from 2005-2007 (N=37). Source of mortality could not be determined for 51% of chick deaths (N=39 chicks).

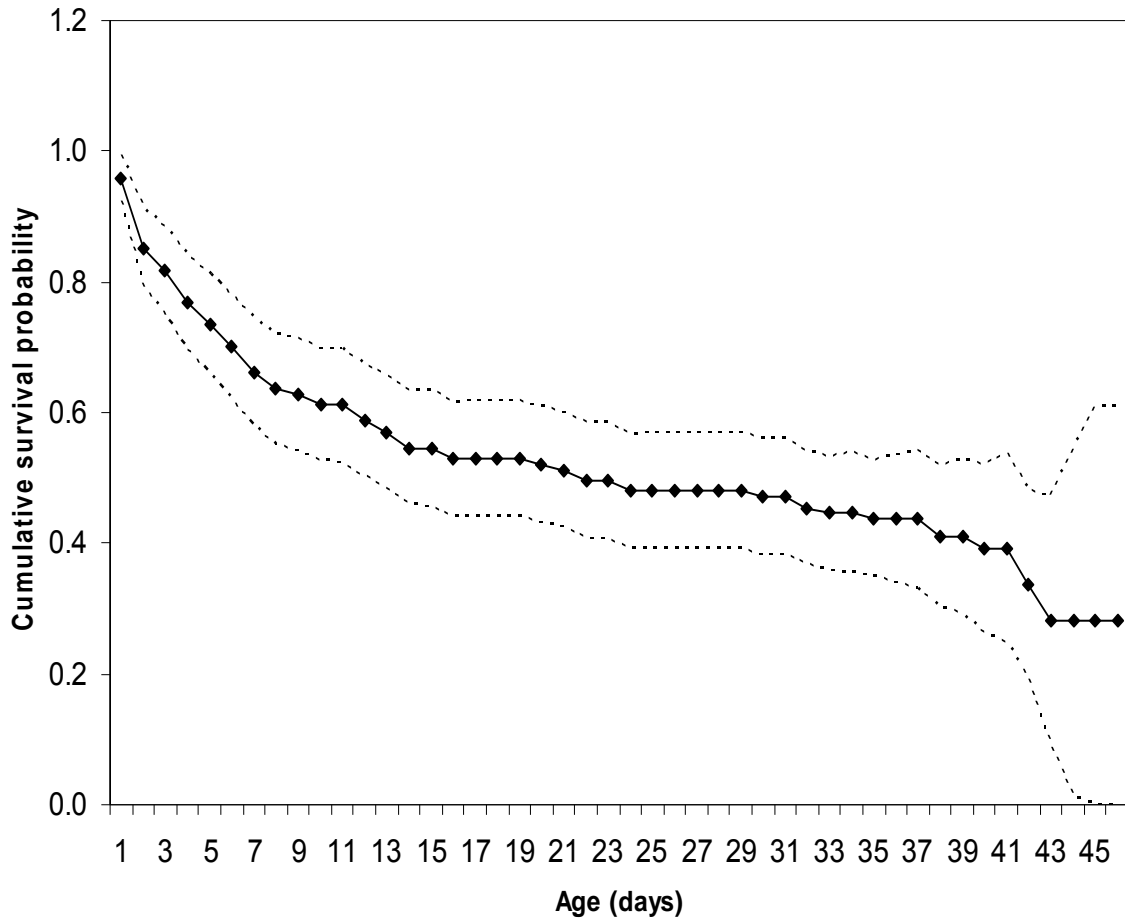


Figure 10.1 Kaplan-Meier survival curve and 95% confidence interval for pre-fledging American Oystercatcher chicks on Cape Hatteras and Cape Lookout National Seashores from 2005 through 2007 (N=121 chicks).

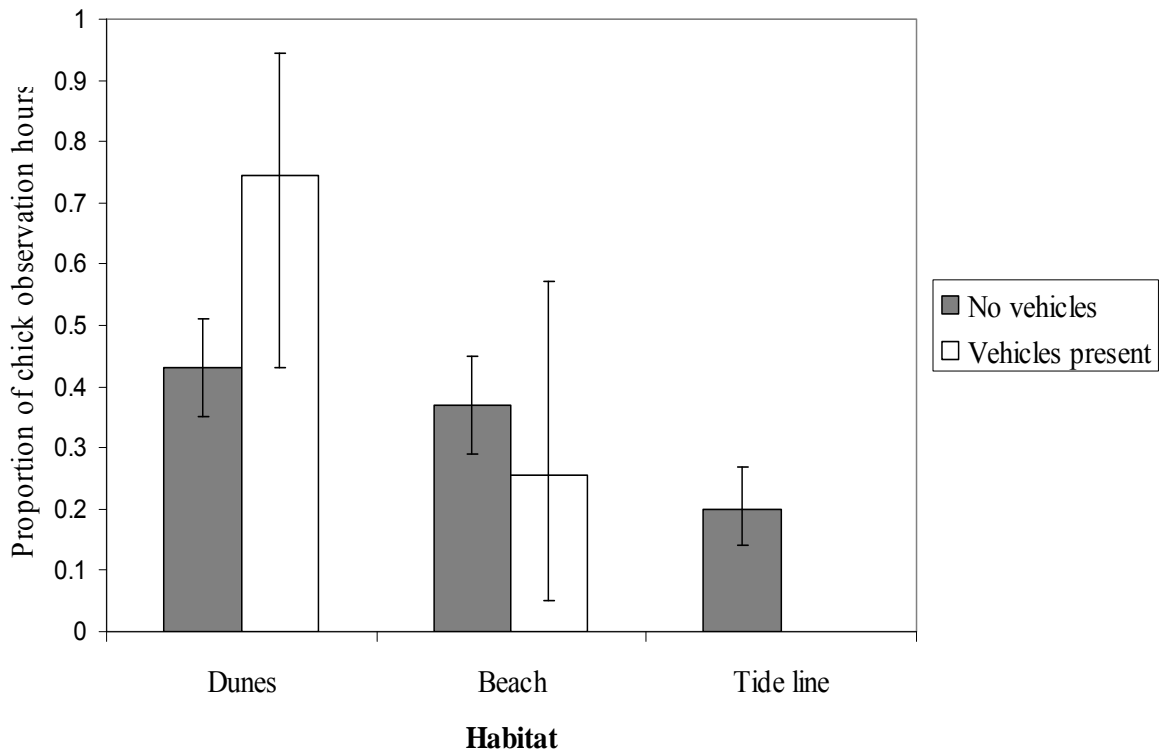


Figure 11.1 Habitat use by American Oystercatcher chicks on Cape Hatteras National Seashore on beaches with and without vehicles present (2004-2007). 54 chicks, 157 observation hours on beaches closed to vehicles, 9 chicks, 12 observation hours on beaches open to vehicles.



Figure 12.1 Radio-marked American Oystercatcher chicks crushed by a vehicle June 16 2005, Cape Lookout National Seashore.

Table 1.1 Model selection results for factors affecting survival of American Oystercatcher nests on Cape Hatteras and Cape Lookout National Seashores from 1999-2008. Models are ranked by  $\Delta\text{AICc}$ .  $W_i$  represents model weight and  $k$  is the number of parameters. Model factors include linear and quadratic daily variation over the nesting season (Day and Day<sup>2</sup>), year, island, presence of off road vehicles, access to foraging areas, and distance to the high tide line.

Model	$\Delta\text{AICc}^a$	$k$	$W_i$	Deviance
Day + Year + Island	0	16	0.294	4807.560
Day + Year + Island + Vehicle	0.015	17	0.291	4805.570
Day + Year + Island + Forage	0.851	17	0.192	4806.406
Day + Year + Island + Tide	1.465	17	0.141	4807.020
Day + Year + Island + Tide + Forage + Vehicle	2.534	19	0.083	4804.080
Day + Year	51.755	11	0	4869.332
Day + Island	56.952	7	0	4882.540
Day	116.954	2	0	4952.548
Day <sup>2</sup>	118.750	3	0	4952.342
Constant	121.374	1	0	4958.968

<sup>a</sup>The lowest AICc score in this model set was 4839.594



Table 2.1 Model selection results for factors affecting survival of American Oystercatcher chicks on Cape Hatteras and Cape Lookout National Seashores from 1999-2008. Models are ranked by  $\Delta\text{AICc}$ .  $W_i$  represents model weight and  $k$  is the number of parameters. Model factors include linear and quadratic daily variation, linear and quadratic age, year, island, presence of off road vehicles, and access to foraging areas.

Model	$\Delta\text{AICc}^a$	$k$	$W_i$	Deviance
Age <sup>2</sup> + Island + Vehicle + Forage	0.000	10	0.991	1018.194
Age <sup>2</sup> + Island + Vehicle	9.442	9	0.009	1029.641
Age <sup>2</sup> + Island + Forage	24.476	9	0.000	1044.675
Age <sup>2</sup> + Island	32.170	8	0.000	1054.374
Age <sup>2</sup> + Year + Island	34.334	17	0.000	1038.474
Age <sup>2</sup> + Year	40.623	12	0.000	1054.804
Age <sup>2</sup>	42.491	3	0.000	1074.711
Day + Age <sup>2</sup>	44.139	4	0.000	1074.356
Day <sup>2</sup> + Age <sup>2</sup>	45.220	5	0.000	1073.435
Age	47.293	2	0.000	1081.515
Day + Age	48.958	3	0.000	1081.178
Day <sup>2</sup> + Age	50.779	4	0.000	1080.997
Day	77.079	2	0.000	1111.300
Day <sup>2</sup>	79.076	3	0.000	1111.296
Constant	91.888	1	0.000	1128.111

<sup>a</sup>The lowest AICc score in this model set was 1038.223

## **Chapter 2**

### **Hurricane disturbance benefits nesting American Oystercatchers**

Abstract:

Coastal ecosystems are under increasing pressure from multiple sources, including human activity, introduced species, and effects of climate change, including sea level rise and increasing storm activity. Hurricanes can be a powerful destructive force, but they also renew barrier island habitat and reset succession. American Oystercatchers are large shorebirds that nest on barrier islands and face threats from habitat loss, human activity, and nest predators. In 2003 Hurricane Isabel altered the landscape of the barrier islands of North Carolina, flattening dunes and creating overwash flats. I compared alternative nest survival models in an information theoretic framework to identify the model(s) that best explained changes in nest survival on two islands of Cape Lookout National Seashore North Carolina from 1998-2007 as well as the temporal extent of any hurricane effect. I compared nest survival in open flat and vegetated dune habitats and measured the extent of the habitat change after the storm. Both islands experienced extensive habitat change during the storm, but nest survival only increased on the island with an apparent reduction in predator activity. When overall nest survival was high or low there was no observed effect of nest placement on nest survival. At intermediate levels nests on open flats survived at a higher rate than nests placed along the dune line. Periodic years with elevated nest survival can help compensate for low annual productivity and may be important for the growth and stability of Oystercatcher populations.

## Introduction:

The manner in which individuals of a given species respond to changes in their environment shapes the distribution, demographics, and ultimately the probability of persistence of that species. Anthropogenic changes can place severe pressure on native ecosystems. As organisms compete with humans and each other for use of remaining habitat, the inherent ability of a species to adapt rapidly to exploit emerging habitats and resources may be critical in determining persistence in a changing environment. The ecological plasticity, or behavioral response to variable resources (Mettke-Hoffman and Greenberg 2005) exhibited by rare or at-risk species is of particular interest when developing conservation strategies (Meyers 1993).

Species that respond rapidly to environmental change tend to be short-lived with high reproductive rates and a broad ecological niche (Sakai et al 2001). Exceptions to this general rule can be found in ecosystems that naturally undergo periodic unpredictable disturbance. The longleaf pine (*Pinus palustris*) depends on fire events to kill competing trees and release dormant seedlings (Platt et al 1988). The light release after a burn allows young longleaf pines to quickly grow into dominant overstory trees. Red-cockaded Woodpeckers (*Picoides borealis*) are, in turn, dependent on mature longleaf pines for nesting sites (Walters 1991). This entire ecosystem is adapted to periodic fire disturbance. Fire adapted ecosystems are common all over the world, particularly in regions with low annual precipitation. In this study I examine evidence that American Oystercatchers (*Haematopus palliatus*) respond to hurricane events in much the same way that many forest and grassland species respond to fire. American Oystercatchers are large, conspicuous shorebirds that nest on islands and

beaches of the Atlantic and Gulf coasts of North America (Nol and Humphrey 1994).

American Oystercatchers are an excellent focal species for long-term research because they are long-lived birds with high breeding site fidelity. Oystercatchers nest in early successional beach habitats with adjacent marshes. Oystercatchers are specialist feeders on intertidal bivalves, so they are closely tied to coastal habitats throughout the year. Typically the species has variable, but generally low nest survival (Nol and Humphrey 1994; Davis et al. 2001; McGowan et al. 2004). American Oystercatchers are listed as species of concern in North Carolina (North Carolina Wildlife Resources Commission 2008) and as high priority species under the US Shorebird Conservation Plan (Brown 2000).

The coastal environment is a constant state of low level change from sand movement via the mechanical processes of longshore transport and overwash. This environment is periodically affected by hurricanes and severe winter storms. These processes create a band of beachfront habitat characterized by bare sand flats, dunes, and early successional plants such as Sea Oats (*Uniola paniculata*) and Seabeach Amaranth (*Amaranthus pumilus*) (Godfrey and Godfrey 1976, Hosier and Cleary 1977). In North Carolina, dune breaks and overwash flats are used by beach nesting birds, including American Oystercatchers (*Haematopus palliatus*), Wilson's Plovers (*Charadrius wilsonia*), the endangered Piping Plover (*Charadrius melodus*), and four tern species. Open flats may offer these species some protection from nest predators as the birds are able to see predators from a greater distance, and the predators must search a large area to locate the nest instead of searching along a narrow beach or dune line. In theory, beach nesting birds should benefit from severe storm events that wash over barrier islands, creating new nesting habitat. Storm events that occur

outside of the nesting season, as hurricanes usually do, should have the greatest positive effect.

The North Atlantic region is currently in a period of increased hurricane activity which is likely to continue for another one to four decades (Goldenberg et al. 2001). Ocean surface temperatures are predicted to increase, driven by multi-decadal oscillations in the North Atlantic and increasing levels of atmospheric greenhouse gases (Emanuel 2005). An increase in ocean temperature is likely to result in increased frequency and intensity of tropical storm systems and could extend the current active hurricane period (Goldenberg et al. 2001; Emanuel 2005; Webster et al. 2006).

On 18 September 2003, Hurricane Isabel made landfall on the Outer Banks of North Carolina as a strong category two hurricane with winds up to 165 km/h, a 2.5 m storm surge, and 4-6 m waves on top of the surge (Bevin and Cobb 2004). Hurricane force wind extended from Morehead City, NC to the southern Virginia coast (fig 1). This hurricane substantially altered the physical structure of some barrier islands of the Outer Banks, flattening dunes and opening wide overwash flats. The eye of the hurricane and the strongest winds in the Northeast quadrant of the storm passed over the island of North Core Banks, part of Cape Lookout National Seashore. Storm intensity was somewhat reduced on islands to the south, including the island of South Core Banks (Bevin and Cobb 2004).

I studied the effects of Hurricane Isabel on the nesting success of American Oystercatchers on North Core and South Core Banks, the two largest islands of Cape Lookout National Seashore. Prior to the storm five years of nest survival data were collected on American Oystercatchers on Cape Lookout National Seashore, identifying mammalian

predators as the primary source of nest failure (Novick 1996; Davis 2000; McGowan 2004, McGowan et al. 2005). Demographic modeling based on mark-recapture and pre-hurricane nest survival data from the Outer Banks projected a high risk of population decline (Schulte and Simons in prep). I hypothesized that the local population must persist through immigration or occasional high productivity years. During the 2004 nesting season following Hurricane Isabel, Oystercatcher nest survival on North Core Banks increased to 475% of the average rate before the storm.

I developed a set of models to evaluate the temporal extent of any hurricane effect and proposed a set of competing hypotheses to explain any changes in nest survival following the hurricane. I monitored breeding Oystercatchers on Cape Lookout through 2007 to track nest survival in the years following the hurricane. I did not, of course, plan for a strong hurricane to hit our study site, so much of the design of this study was necessarily developed after the event. I used the hurricane to learn as much as possible about the response of oystercatchers to a sudden change in their environment.

Our null hypothesis was that estimates of the probability of nests surviving to hatching stage would not differ between pre-hurricane and post-hurricane years. Alternatively, I suspected that I might detect differences in estimates of probabilities of nest success among years. I constructed a set of models with different temporal patterns of nest survival to evaluate how long any effects of the hurricane would last.

Next, I proposed three hypotheses about the mechanisms that may have affected the different probabilities of nest survival. Hypothesis 1: Oystercatchers shifted their nest locations to higher quality habitat, leading to decreased depredation rates. Hypothesis 2: The

spatial arrangement of oystercatcher nests became more variable after the habitat changed and resulted in lower depredation rates. Hypothesis 3: Predator populations were directly reduced by the hurricane, resulting in lower depredation rates.

#### Methods:

##### *Study area*

Cape Lookout National Seashore is comprised of a narrow string of barrier islands running 90 kilometers south from Ocracoke Inlet to Bogue Inlet, North Carolina. Cape Lookout is one of the few remaining undeveloped barrier island chains on the Atlantic coast. Cape Lookout is not connected to the mainland by bridges and consequently sees fewer visitors than better known Cape Hatteras National Seashore to the North. Several small commercial ferry services bring visitors and vehicles to the park. Vehicle ferries run from March through November. Off road vehicles are permitted on beach and interdune roads in the park except in designated wilderness areas or sensitive bird or turtle nesting areas.

The islands are characterized by wide barrier beaches backed by a primary and secondary dune complex broken by flats and overwash fans. The dunes fade into wax myrtle (*Morella cerifera*) scrub and then to spartina saltmarsh bordering the back bays and sounds. Cape Lookout supports approximately 60 breeding pairs of Oystercatchers. Our study area includes the islands of North Core Banks and South Core Banks (Fig. 1). North Core Banks is 29 kilometers long and supports 16-22 nesting pairs of Oystercatchers. South Core Banks is 35 kilometers long and supports 24-27 nesting pairs.



### *Field Methods*

The breeding season for American Oystercatchers in North Carolina begins in late March and runs through early August. Nests were located by watching for false incubation and alarm calling, specific behaviors that indicated a nest was nearby. Once in the nest area, observers located nest scrapes by following Oystercatcher tracks or by systematic searching. Observers followed minimal site disturbance practices including using natural features as nest markers, never walking directly to a nest and spending minimal time in the nest area. Nests were monitored every one to four days until hatching or nest failure. If a nest failed, the observer attempted to determine the cause by searching the nest area for signs of predators, flooding, human activity, or other evidence associated with the failure. The proportion of unidentified nests in each year varied due to differences in observers and frequency of nest checks between years and islands. To facilitate comparison between years and islands, unidentified failures were allocated proportionally to known sources of failure. Unidentified nests were not allocated to the storm overwash category since storm-related failures were easily identified and did not contribute to the unidentified nest pool.

### *Analysis*

I modeled daily nest survival on North Core and South Core Banks from 1999 through 2007 to evaluate the temporal and spatial extent of any hurricane effects across the study area. I compared five alternative models in Program Mark (White and Burnham 1999) including three proposed hurricane effects models. Model one ( $S_{\cdot}$ ) was a null model of constant survival. Model two ( $S_{\text{time}}$ ) was a fully time dependant model with separate parameters for each year. Model three ( $S_{\text{base} + \text{hurricane}}$ ) had two nest survival parameters; a

baseline survival rate (all non-hurricane years), and a single year increase in 2004 after the hurricane. Model four ( $S_{\text{base} + \text{hurricane} + \text{post1}}$ ) included an additional parameter for a “carry-over” year of intermediate nest survival following the initial increase. Model five ( $S_{\text{base} + \text{hurricane} + \text{post2}}$ ) allowed a two-year carryover effect before returning to the baseline survival level. I assessed the effect of the hurricane on nest survival on both of our study islands. I constructed five models with data pooled from both islands, then included every combination of temporal models for both islands separately. I used Program Mark to rank and compare all 30 alternative models using Akaike’s Information Criteria (AIC) (Akaike 1973) in an information theoretic framework. The nest survival model in Program Mark uses a maximum likelihood method to estimate daily survival rates when time between nest checks is greater than one day. This method is less biased than apparent nest survival (successful nests divided by total nests monitored) as it accounts for nests that failed and were never found. The average incubation period for Oystercatcher nests is 27 days (Nol and Humphreys 1994). To obtain nest survival probabilities I raised estimates of daily survival rates to the 27<sup>th</sup> power. I report on the outcomes of 699 nests monitored from 1999-2007.

I quantified habitat change from Hurricane Isabel using orthorectified aerial photos of Cape Lookout (USGS 1998, NCDOT, 2003) to delineate the extent of open sand flats before and after the storm. A complete aerial survey of the Seashore was conducted in January 1998 and again in September 2003 shortly after Hurricane Isabel. The extent of the open sand flat habitat available for nesting was calculated by heads-up digitizing of open sand habitat using ArcGIS Desktop version 9.1 (ESRI 2006)

For each year and island I calculated the proportion of oystercatcher nests on sand

flats and in the relatively linear habitat of the upper beach and dunes. I then used habitat type as a covariate in the best temporal nest survival model. For the purpose of this analysis I assumed no within-habitat heterogeneity in survival probabilities throughout the incubation period.

Opportunistic observations suggested that raccoons and other mammalian predators followed landform features like dune lines and habitat edges. When Oystercatchers nests were lined up along the base of the dunes they appeared to be easy targets for predators. After the hurricane the Oystercatchers had more opportunity to move out onto open flats and dune breaks. I hypothesized that increased variability in nest placement would increase overall nest survival for a given island and year. I measured variability in nest placement using the mean deviation of the distance of nests to the high tide line. For each year I calculated the mean distance of nests to the high tide line for each island, and found the mean of the absolute value of the residuals, or mean deviation. I used mean deviation instead of standard deviation to minimize the effect of the skewed distribution of distance values resulting from the habitat bounded on one side by the ocean and broken occasionally by large flats on the other.

I noted predator sign (tracks, scat, and sightings) during the nesting season as an indicator of predator activity near oystercatchers nests. Tracks from mammalian nest predators are easily visible on the sandy beaches and flats of Cape Lookout, but they are quickly erased by wind and rain. I assumed that tracks observed during subsequent nest checks were newly created. I did not assume that the abundance of predator sign was a direct indicator of true predator abundance, but that it provided some indication of the overall

predator activity level for each island and year in the habitat where Oystercatchers were nesting. Our observations allowed us to document presence/absence and a qualitative assessment of relative predator activity on each island.

### Results:

Our model results indicate that the effect of Hurricane Isabel on nest survival varied between islands. The best model with 60% of model weight indicated that North Core Banks experienced a hurricane effect with a two-year carry-over effect, while nest survival on South Core Banks was best described by a simple year effects model (Table 1). Nest survival on North Core Banks increased from the baseline rate of 0.170 (SE 0.021) to 0.772 (SE 0.090) in 2004. Nest survival averaged 0.43 (SE 0.081) for two years after the initial increase. Nest survival did increase on South Core Banks after the hurricane, but the increase was not outside the range of annual variation (Fig. 2).

Both islands experienced extensive habitat change from overwash and wind (Fig. 3). Delineation of habitat type on ortho-rectified aerial photos from before and after the hurricane revealed that the total area of sand flats on North Core Banks increased by 31% from 382 to 501 hectares. The amount of open sand flat habitat increased by 100-200% over much of this island, but there was significant erosion of a large flat at the north end of the island which reduced the total area of open flats. On South Core Banks, the area of open sand flat habitat increased by 110% from 52 to 109 hectares.

Oystercatcher pairs shifted nesting locations after the hurricane. On North Core Banks the average distance of a nest from the high tide line increased from 92.7 meters (SE

5.14) before the hurricane to 150.2 meters (SE 21.6) after the storm, as Oystercatcher pairs moved away from the beach and onto overwash flats. On South Core Banks, the mean distance from nest to high tide line increased from 49.3 to 71.1 meters in the year after the hurricane. There was no apparent shift in the proportion of birds nesting on dunes versus flats for either island (Fig 4).

The variability in the spatial arrangement of nests increased on both islands after the hurricane. The mean residual distance from the mean distance of nests to the high tide line increased from 53.1 meters (SE 3.56) to 82.8 meters (SE 13.5) on North Core Banks, and from 28.8 (SE 1.91) to 51.6 (SE 8.67) on South Core Banks.

I incorporated nest habitat as a covariate in the best temporal survival model to determine if habitat type affected nest survival. The habitat covariate did not substantially improve the best model (0.1608 decline in  $\Delta$ AIC), indicating that habitat type was not a useful indicator of overall nest survival. Despite the lack of overall predictive ability, I found that the effect of habitat varied by year (fig 5). On North Core Banks before Hurricane Isabel overall nest survival was low ( $< 0.34$ ), and I found no difference in nest survival on open flats (0.161, SE 0.020) and in the dunes (0.160, SE 0.017), with confidence intervals for nest survival in each habitat fully overlapped the mean survival rate for the other habitat. When overall nest survival was high ( $> 0.66$ ) in the year immediately following the hurricane there was still no difference between habitats, with open flat nest survival at 0.859 (SE 0.162) and dune nest survival at 0.731 (SE 0.116). During the period of intermediate nest survival ( $0.33 < S < 0.67$ ) after the storm the survival rate for nests on open sand flats was 0.600 (SE 0.112), while the survival rate for nests in the dunes was 0.243 (SE 0.094). On South Core

Banks where I did not find an effect of the hurricane on nest survival, there was no difference in survival between nests on sand flats and those in vegetated dunes.

Mammalian depredation accounted for 57% (SE 1.9%) of all nest fates, and 74% (SE 1.9%) of all nest failures. Storm overwash was responsible for an additional 12% (SE 1.4%) of nest failures, while the remaining nests losses were attributable to avian predators, ghost crabs, and human activity. The source of failure could not be identified for 50% (SE 2%) of all nest failures. The proportion of nests lost to mammalian depredation varied across years and between the islands (fig 6 and 7). On North Core Banks during non-hurricane years 58% (SE 3%) of all nests laid were lost to mammalian depredation. In the first year after Hurricane Isabel this number dropped to 20% (SE 8%). Over the next two nesting seasons mammalian depredation remained low at 15% (SE 5.8%). On South Core Banks mammalian depredation accounted for 62% (SE 2.4%) of all nests laid over the study period. There was no evidence for a reduction in mammalian depredation on South Core Banks after Hurricane Isabel.

General observations of predator activity corresponded to observed rates of nest depredation. Mammalian predator sign was frequently observed on North Core Banks from 1999 to 2003 with tracks and sightings over the entire island throughout the nesting season. In 2004 we did not observe any predator sign until the second week in May, four weeks into the nesting season. Raccoon (*Procyon lotor*) and Feral Cat (*Felis catus*) tracks were observed occasionally during the second half of the season, but only near a group of rental cabins, the main center of human activity on the island. In 2005 and 2006, the frequency of predator tracks and sightings increased on North Core Banks. Tracks were common in every

month of the nesting season near the cabins, as well as locally at several other sites comprising approximately 25% of the island. By the 2007 nesting season, predator activity on North Core Banks was back to the pre-hurricane level with tracks observed over the entire length of the island throughout the nesting season. On South Core Banks Raccoon tracks were observed during the entire nesting season from April to August over the entire island in all years. Raccoon sightings were common, particularly near centers of human activity.

#### Discussion:

The wind and wave action from Hurricane Isabel had a strong effect on the physical characteristics of the islands of Cape Lookout National Seashore, resetting succession and altering dune lines. Effects on wildlife populations on Cape Lookout were somewhat more complex. Despite similar physical changes to both of our study islands, North Core and South Core Banks, the change in the survival rate of American Oystercatcher nests was quite different between the two islands.

Nesting success on North Core Banks was affected by changes from Hurricane Isabel. Our best model of the temporal effects of the hurricane on nest survival included three parameters for North Core Banks: A parameter for constant survival for non-hurricane years (1999 to 2003 and 2007), A parameter for a single-year increase in survival after the hurricane (2004), and a parameter for two years of intermediate nest survival before returning to the baseline level. The same model data includes separate parameters for each year for the island of South Core Banks, indicating that any changes in nest survival on this island are within the range of annual variation.

Our first explanatory hypothesis for the observed changes in nest survival stated that increased availability of open flat habitat would lead to increased nest survival. This hypothesis reflected our expectation that nests on open sand flats were harder for predators to find. Incubating Oystercatchers leave the nest as soon as they detect a nest predator, relying on the cryptic coloration of the eggs for protection. On extensive open flats, nest predators such as Raccoons and Cats must search the entire flat as opposed to the relatively narrow dune line and upper beach habitats where Oystercatchers also nest.

The hurricane increased the amount of open flat nesting habitat on both islands, and mean distance of nests from the high tide line increased, suggesting that Oystercatchers shifted further from the beach and onto newly created sand flats. The proportion of nests in each habitat did not change, however, which may indicate that the resident territory holders were able to defend the expanded sand flats. Pairs without prior access to sand flats remained in the dune habitat, while sand flat nesters were able to move closer to sound-side foraging areas and away from human disturbance on the beach. Still, our first hypothesis found little support. I found no difference in survival between dune and beach nests before the hurricane where overall nest survival was low, or after the storm where overall nest survival was high. Habitat specific nest survival differed only at an intermediate level of overall nest survival. After the initial increase following the hurricane, nest survival on North Core Banks began to decline back toward the baseline rate. Nest survival in the dune habitat immediately dropped to pre-hurricane levels, but survival of nests on the flats remained high for three years after the storm. If habitat quality were driving the overall increase in nest survival I should have observed a habitat specific difference in survival immediately after the



storm. Furthermore, both islands experienced substantial habitat change, but nest survival only increased on North Core Banks.

Our second hypothesis, increased variability in the spatial arrangement of oystercatcher nests resulted in less depredation, also found little support in our data. I predicted that increased variability in nest placement would benefit nesting oystercatchers. Prior to the hurricane many of the oystercatcher nests were arranged in a linear pattern along the dune line. Raccoons were often seen traveling along the dunes and apparently had little difficulty finding oystercatcher nests. Variability in nest placement was represented by the mean deviation from the mean distance from the high tide line. High tide lines were mapped each year, so I used this metric as a consistent way to compare overall variability in nest placement among years. Variability in nest placement increased on both islands after the hurricane, but nest survival only increased on North Core Banks. Habitat changes and spatial arrangement were therefore not likely to be the primary factors affecting changes in nest survival.

Our third explanatory hypothesis suggested that the increase in nest survival could be explained by a reduction in mammalian predator populations during the storm. Unfortunately I had no quantitative estimate of predator populations at any point in our study. I used the proportion of nests taken by mammalian predators and field observations of predator sign to evaluate the relative change in predator activity before and after the hurricane. Our observations of predator activity on both islands corresponded to documented changes in the proportion of nests taken by mammalian predators. On South Core Banks I found no significant pattern in the proportion of nests taken by mammals associated with the

hurricane. Predator activity remained high on South Core Banks through the course of the study. Signs of predators, including tracks and sightings disappeared almost entirely on North Core Banks the year after the hurricane, while the proportion of nests lost to mammals dropped from 58% to 20%. Without quantitative estimates of predator abundance I cannot definitively say that Hurricane Isabel reduced predator populations on North Core Banks. Still, there was a clear association between lower observed predator activity, fewer nests taken by mammals, and increased overall nest survival.

The difference in apparent predator abundance on North Core and South Core Banks after the hurricane may be explained by a difference in the physical character of the islands. North Core Banks is very low lying and much of the island was completely overwashed during the hurricane. Many of the Raccoons and Feral Cats on North Core Banks may have drowned during the storm. South Core Banks is wider at the south end, and has considerably more upland habitat where raccoons and other mammalian predators could take refuge.

The interaction between habitat type and rate of overall nest survival could be explained by differences in predator activity. When predators are active in the nesting zone most nests fail no matter where they are located. If enough predators are searching, a nest is likely to be found even if it is in a good location. Conversely, when there are few mammalian predators in the nesting zone, most of the nests survive in all habitats. Habitat becomes important when predators are at an intermediate level as many of the obvious dune and beach nests are found, but harder to locate nests on flats survive. I observed this effect on North Core Banks in 2005 and 2006 as predator activity began to increase again after the hurricane.

These findings have implications for developing conservation strategies for other beach-nesting birds, especially when humans intervene to return to beach habitats to their pre-hurricane state. On developed barrier islands, new overwash habitat created by storms is often quickly removed as roads are re-built and artificial dunes are created to protect roads and structures. This has the effect of negating much of the benefit of storms for beach nesting birds. Introduced nest predators and artificially abundant populations of native predators are increasingly common in the coastal zone, even on remote sites like Cape Lookout. Management efforts to control predator populations may be particularly effective if they coincide with natural habitat creation from major storms. Well-designed studies of barrier island predator communities would significantly improve our understanding of predator-prey interactions in these systems.

Major storms clearly have the potential to affect Oystercatcher nest survival by creating new nesting habitat and reducing predator populations. High reproductive success subsequent to major storms may be important to the long term growth and stability of Oystercatcher populations. Demographic modeling suggests that periodic years with high reproductive success can offset or reverse population declines depending on the baseline reproductive rate and the frequency of the high production years. Thus, although sea level rise associated with global warming may reduce habitat for coastal birds in some areas, our findings suggest that increased habitat disturbance from more frequent hurricanes may benefit species associated with these dynamic environments.

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Table 2.1 Model ranks for the top five models for temporal effects of Hurricane Isabel on American Oystercatcher nest survival, Cape Lookout National Seashore, North Carolina

Model	AICc	$\Delta$ AICc	Weights	Likelihood	K	Deviance
(S <sub>NCB</sub> (base+hurricane+post2) + SCB(year))	2892.79	0	0.602	1	12	2868.76
(S <sub>NCB</sub> (base+hurricane+post2) + SCB(base+hurricane+post2))	2895.78	2.988	0.135	0.224	6	2883.77
(S <sub>NCB</sub> (base+hurricane+post2) + SCB(base+hurricane+post1))	2896.22	3.426	0.109	0.180	6	2884.21
(S <sub>NCB</sub> (base+hurricane+post1) + SCB(year))	2897.72	4.929	0.051	0.085	12	2873.69
(S <sub>NCB</sub> (year) + SCB(year))	2898.61	5.817	0.033	0.055	18	2862.53

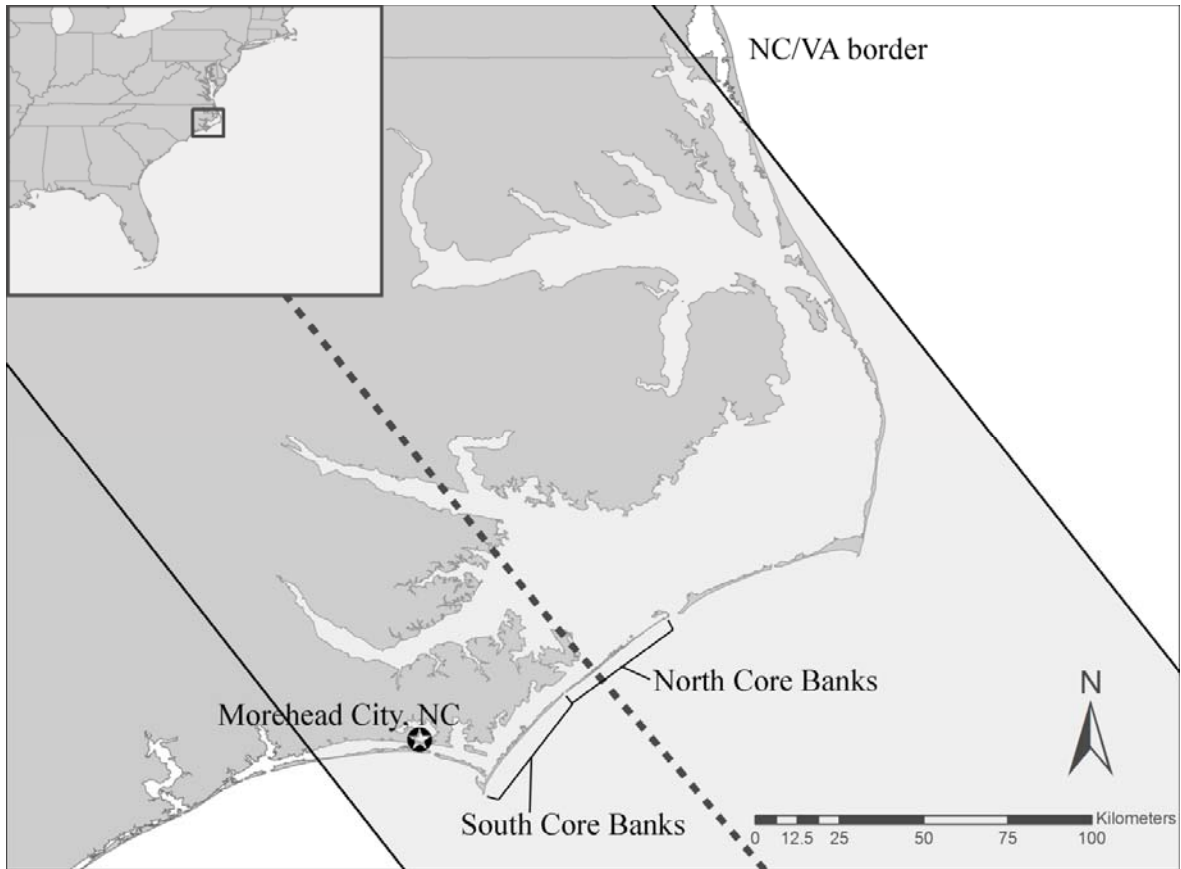


Figure 1.2. Study sites on Cape Lookout National Seashore, Carteret County, North Carolina, showing the track of Hurricane Isabel and hurricane-force wind field.



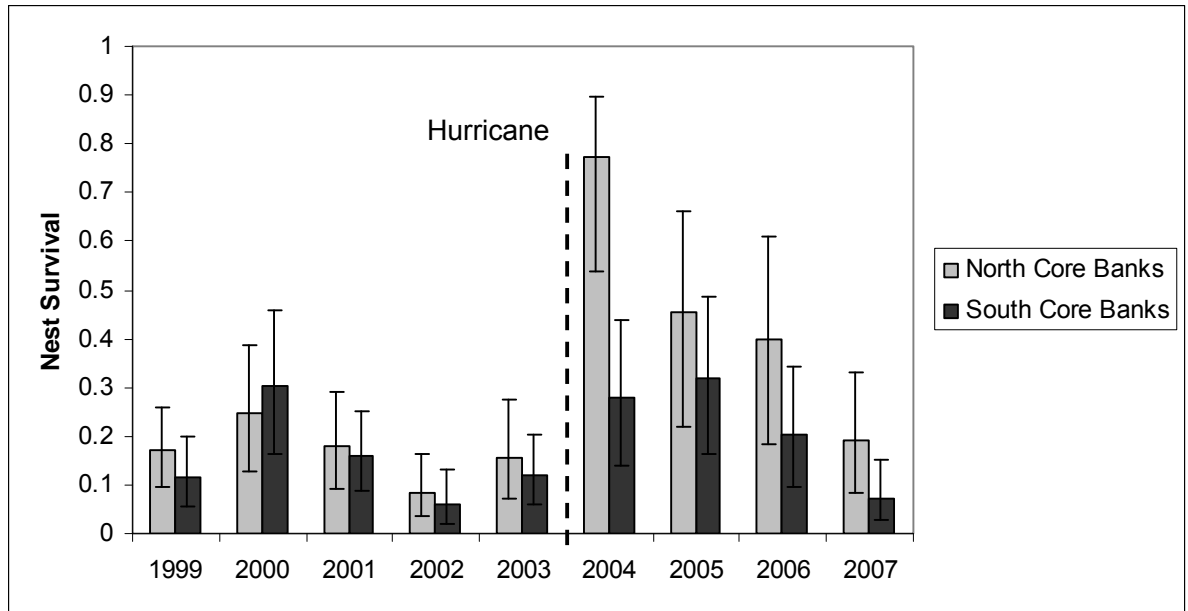


Figure 2.2. American Oystercatcher nest survival on two islands of Cape Lookout National Seashore before and after Hurricane Isabel. Error bars represent 95% confidence intervals for the survival estimates.

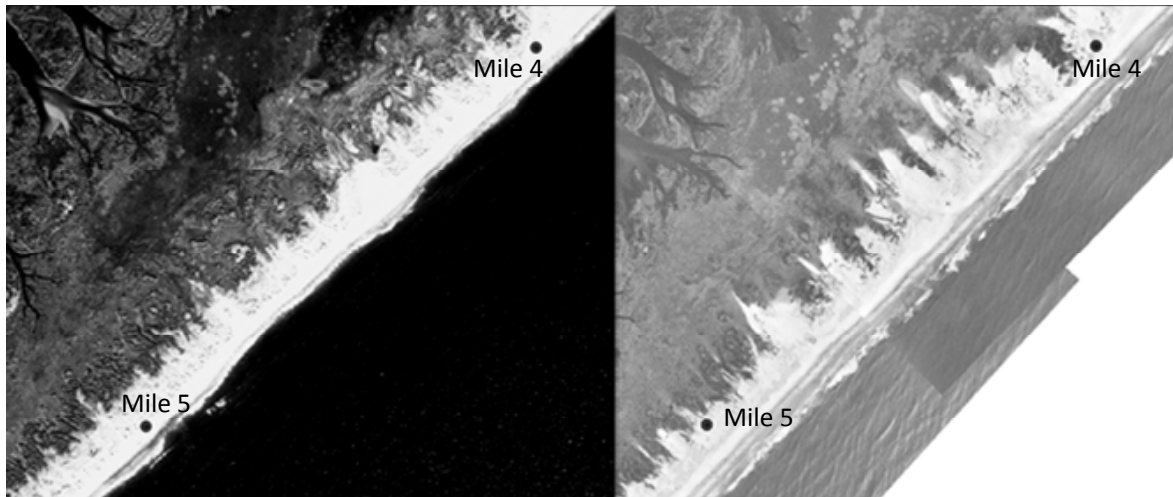


Figure 3.2. A section of North Core Banks in 1998 (left) and 2004 (right) showing overwash and dune breakup caused by Hurricane Isabel in 2003. NPS mile markers are used as reference points.

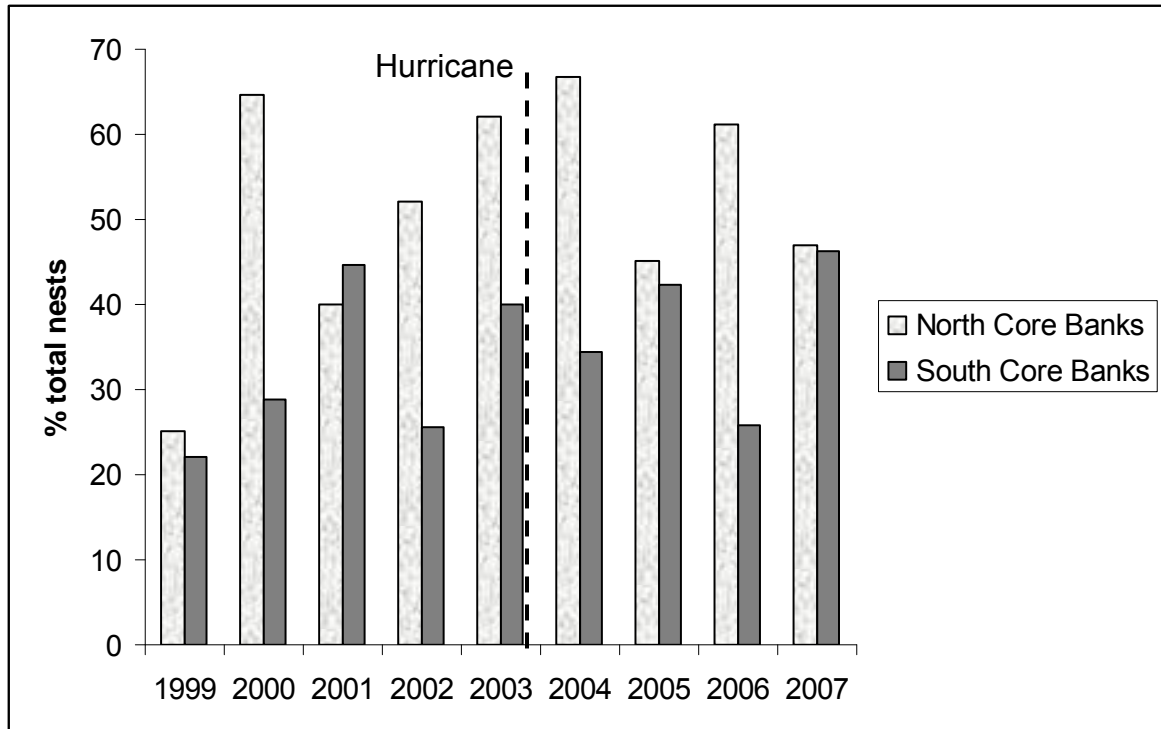


Figure. 4.2. Percentage of nests on open sand flats on two islands of Cape Lookout National Seashore

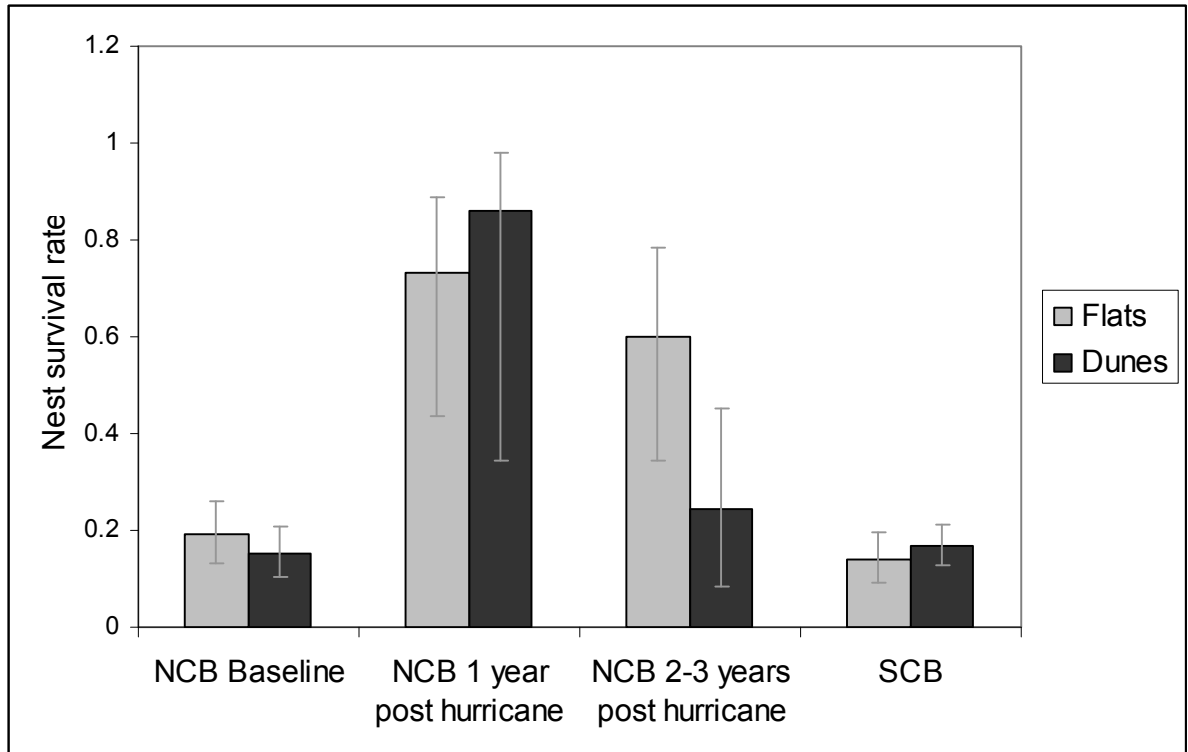


Figure 5.2. Habitat-specific survival for American Oystercatcher nests on sand flats and in vegetated dunes on North Core Banks (NCB) and South Core Banks (SCB), Cape Lookout National Seashore. Error bars represent 95% confidence intervals.

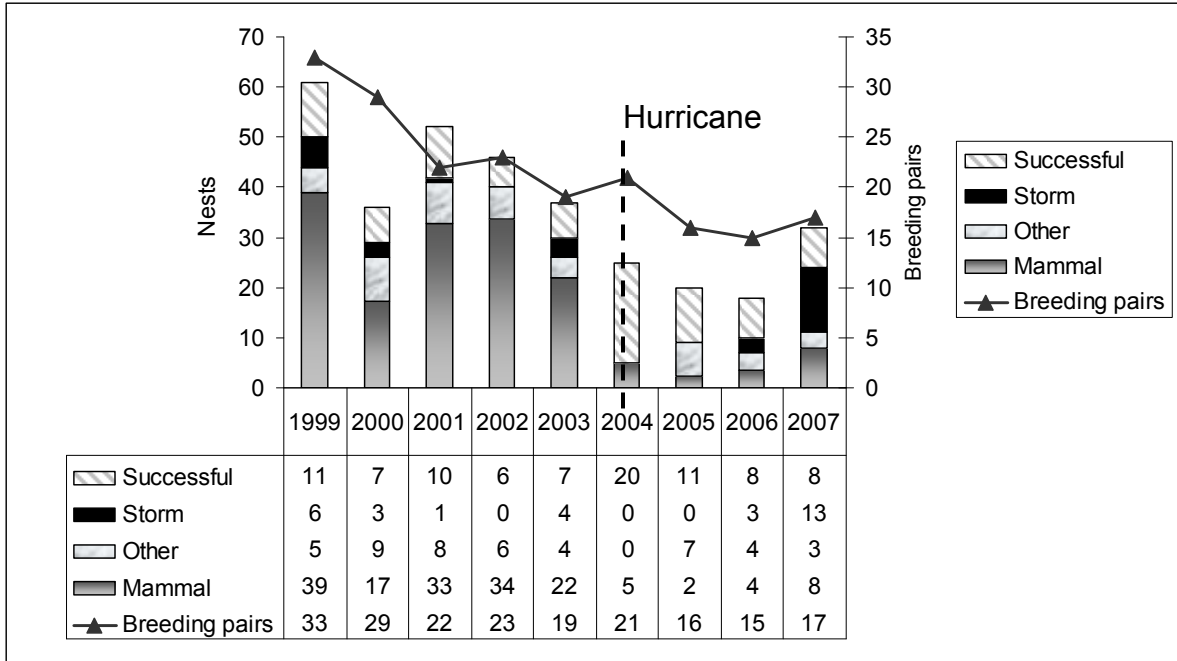


Figure 6.2. Nest fates for oystercatcher nests on North Core Banks, Cape Lookout National Seashore from 1999 - 2007

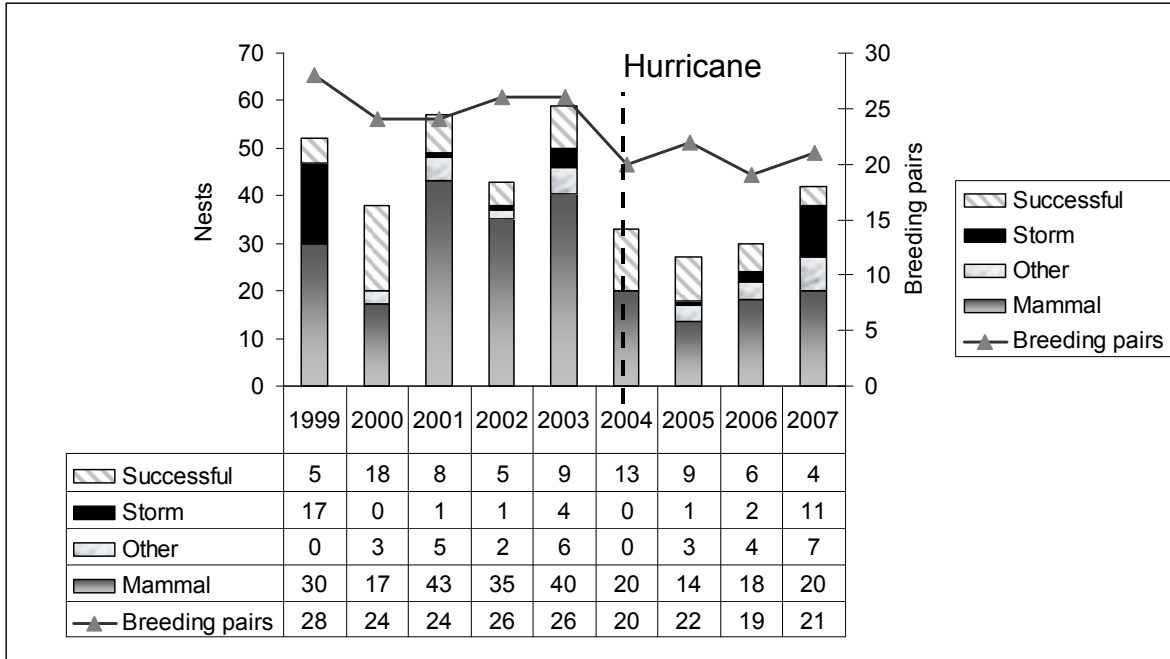


Figure 7.2. Nest fates for oystercatcher nests on South Core Banks, Cape Lookout National Seashore from 1999 - 2007

### **Chapter 3**

**A demographic model for American Oystercatchers that incorporates stochastic  
hurricane events**

Abstract:

I developed a set of demographic models for the American Oystercatcher (*Haematopus palliatus*) population in North Carolina to assess the effects of periodic hurricanes on population growth. American Oystercatchers are rare, long-lived shorebirds that breed and winter on the Atlantic and Gulf coasts of the United States. Nesting success, increased from 20%, to 80% on Cape Lookout National Seashore after a category two hurricane crossed the island in 2003. I constructed a baseline stochastic population model without hurricane effects and two alternative parameter sets (10 and 15 year hurricane events) based on hurricane strike probabilities for North Carolina counties. Model parameters (survival, fecundity, age of first breeding), were estimated from mark-recapture data, a twelve year breeding study, and literature sources. The baseline model had the lowest population growth rate ( $\lambda = 0.986$ ) with an average population decline of 49% over 50 years. The 15 year hurricane model reversed population decline ( $\lambda = 1.0029$ ) with an average increase of 15.3% over 50 years. When hurricane frequency increased to 10 years, the oystercatcher population increased by 63.9%,  $\lambda = 1.0099$ . Our results show that hurricane frequency affects population growth and suggest that American Oystercatcher nesting and territory acquisition strategies may have been shaped by periodic hurricanes which improve habitat, and reduce predator populations.



## Introduction:

The frequency and intensity of tropical cyclones are expected to increase in coming decades as warming ocean temperatures extend the current active hurricane period. (Goldenberg et al. 2001, Emanuel 2005 Webster et al. 2006). Hurricanes can have devastating effects on coastal communities, both human and natural. The consequences can be especially severe for endemic tropical island species (Waide 1991, Walters 1991, Wiley et al. 1994, Lewis 1995; Carter et al. 2000).

Nevertheless, the ecological changes associated with global warming will produce winners as well as losers. In many cases the species that are predicted to benefit from climate change are widespread, adaptable organisms that can easily shift their range (Thuiller et al. 2008). This is especially true for invasive species such as Argentine ants (*Linepithema humile*) and Kudzu vines (*Peuraria lobata*) (Dukes and Mooney 1999). Much less common are examples of climate change benefiting species that are currently at risk. Climate change in the form of more frequent hurricanes may be detrimental for tropical island endemics, but the effects could be quite different for barrier island ecosystems. Species that are adapted to exploit early successional beach habitat should benefit from more frequent hurricanes as storm overwash and sand movement are a normal part of barrier island dynamics (Godfrey 1976). Early successional plants like Sea Oats (*Uniola paniculata*) and Seabeach Amaranth (*Amaranthus pumilus*) depend on storm overwash to create a bare sand environment where they have a competitive advantage. Dune breaks and overwash flats are used by beach nesting birds, including the American Oystercatcher (*Haematopus palliatus*). American Oystercatchers are large, long-lived shorebirds that are closely tied to the coastal zone

throughout the year. Unlike many shorebirds that breed in the Arctic and migrate to South America, Oystercatchers nest on the Atlantic Coast from Cape Cod to Florida, and on the Gulf Coast from Florida to Mexico (Nol and Humphrey 1994). The winter range extends south from Long Island, New York through the Gulf coast. The US Shorebird Conservation Plan lists American Oystercatchers as a high priority species, in part because of significant threats to habitat from coastal development and heavy recreational use of breeding habitats (Brown et al. 2001). Like many long lived species, oystercatcher reproductive rates tend to be highly variable but generally low (Evans 1991, Nol and Humphrey 1994, Davis et al. 2001, McGowan 2004, van de Pol 2006). A species with low productivity and high adult survival avoids rapid population swings, but has limited ability to recover quickly from population declines.

We studied American Oystercatchers on the Outer Banks of North Carolina from 1999 through 2007, and found that a variety of factors affect Oystercatcher reproductive success including nest predators, weather patterns, flooding events, proximity to food sources, and human activity. Exceptionally high reproductive success following a hurricane in 2003 suggested that disturbance from hurricanes may periodically provide the conditions necessary for elevated nesting success (Schulte and Simons in revision). Specifically, hurricane overwash creates optimal nesting habitat, opens access to foraging areas, and reduces populations of mammalian nest predators. American oystercatchers evolved in an environment shaped by severe storms and appear to have several adaptations that allow them to take advantage of periodic hurricane disturbance. Sub-adult oystercatchers can use new nesting areas created by storms to establish a territory and join the breeding population.

Breeding Oystercatchers produce more chicks than they can successfully fledge in most years, which allows for an immediate increase in productivity in a post-hurricane environment with better foraging opportunities and fewer predators.

In this chapter I present a demographic model for American Oystercatchers to assess the relationship between hurricane disturbance and American Oystercatcher population growth rates. Prior to this study, many basic demographic parameters were unknown for American Oystercatchers. Estimates of juvenile survival, subadult survival, and recruitment are still preliminary, but they allow comparisons to published estimates for the similar and intensively studied Eurasian Oystercatcher (*Haematopus ostralegus*).

Reproductive success of American Oystercatchers has been better documented (Nol 1989, Davis et al. 2001, McGowan et al. 2005, Sabine et al. 2006, Traut et al. 2006, Schulte and Simons in prep), and in recent years, coordinated, widespread banding and re-sighting efforts along the Atlantic coast have provided insights into connections between breeding and wintering sites, return rates, and apparent adult survival rates. I used six years of mark-recapture data from the Outer Banks of North Carolina to estimate apparent adult survival and age of first breeding.

### Methods:

#### *Study Sites*

Cape Lookout and Cape Hatteras National Seashores (Figure 1) form a thin string of barrier islands that jut out into the Atlantic Ocean along the coast of North Carolina. Together, the parks comprise over 160 km of barrier islands habitats. The islands are characterized by wide barrier beaches backed by a primary and secondary dune complex

broken by flats and overwash fans. The dunes fade into wax myrtle (*Myrica cerifera*) scrub and then to saltmarsh bordering the back bays and sounds. This system is subject to periodic washover and recovery events (figure 2). Cape Lookout and Cape Hatteras support approximately 90 breeding pairs of Oystercatchers which nest on the sand flats and dunes and forage along the beach and salt marsh. Off road vehicles are permitted on beach and interdune roads in both parks except in designated wilderness areas or sensitive bird or turtle nesting areas. Cape Hatteras has a permanent road system and several small towns along the length of the islands.

#### *Analysis and model development*

I constructed a four-stage matrix model with juvenile (post-fledging), subadult 1 (second year), subadult 2, and adult (breeding) stages (Figure 3). The model includes six demographic parameters: fecundity ( $F$ ), juvenile survival ( $S_j$ ), subadult<sub>1</sub> survival ( $S_1$ ), subadult<sub>2</sub> survival without transition ( $S_2$ ), subadult<sub>2</sub> survival with transition to adult ( $T_{s2}$ ), and adult survival ( $S_a$ ) (Figure 3).

I used Program Matlab (Mathworks 2005) to create a basic deterministic matrix model to find the stable stage distribution, and the sensitivity of lambda to each of the matrix elements. I then simulated annual stochasticity by using the variance of each parameter estimate to draw a value for each year of the simulation from an appropriate distribution. The initial population size (678 breeding adults) was set using the most recent estimate of breeding adults in North Carolina (Cameron and Allen 2007). The initial population size was set at 1255 individuals based on a stable age distribution with adults comprising 54% of the total population.

Baseline and alternate input parameters were derived from both published and unpublished sources for the American Oystercatcher, as well as published literature on the closely related European Oystercatcher. Adult survival was calculated from six years of mark-resight data on the Outer Banks using the Cormack-Jolly-Seber (recaptures only) model in Program Mark (White and Burnham 1999). I examined four separate models where survival ( $\phi$ ) and capture probability ( $\rho$ ) were either time-dependent or constant ( $\phi_t\rho_t$ ,  $\phi_t\rho$ ,  $\phi\rho_t$ ,  $\phi\rho$ ). I used the weighted average of the estimable survival values to obtain an estimate of apparent adult survival of 0.89 (SD 0.03). I used Program Mark to estimate the underlying process variance to avoid inflating the estimate of standard deviation. This program uses the equations for estimating variance components described in Gould and Nichols (1998) and White et al. (2001). Sampling variance accounted for 53% of total variance in survival. The apparent survival rate obtained through annual resight records does not account for emigration from the study area. Although oystercatchers have high site fidelity, they can be driven off their territory by other oystercatchers, or abandon the site if the habitat becomes poor. Survival studies for the similar European Oystercatcher suggest that apparent survival may be biased low by 3-10% (Goss-Custard et al. 1982). Therefore, I used 0.92 (SD 0.03) as our estimate of adult survival for American Oystercatchers. I set subadult survivorship to equal adult survivorship because I was not able to estimate it directly from the available mark-recapture data. This is likely a reasonable approximation as oystercatchers can remain in the subadult stage for several years and are functionally adults by their second year. This estimate is slightly lower than the Ens et al. (1995) estimate for European Oystercatchers,

and between the two values Durell and Goss-Custard (1996) used for younger and older subadult survivorship of European Oystercatchers in their model.

Estimates of the rate of subadult transition to adult, and juvenile survival were based on published studies of the European Oystercatcher. Subadults that survive each year either remain as non-breeders or they transition to breeding adults; thus, overall subadult survivorship is composed of two separate transition probabilities. Ens et al. (1995), Heg et al. (2000), and van de Pol et al. (2007) discuss in detail the processes and decisions involved when nonbreeding oystercatchers attempt to acquire a breeding territory. The age of first breeding for Eurasian Oystercatchers was quite variable, ranging from 3-11 years. After an oystercatcher reached age two, the probability of surviving and becoming a breeder was 19%, while the probability of surviving and remaining a nonbreeder was 72% (Ens et al. 1995). Safriel et al. (1984) reported recruitment to a breeding population over a 15-year period; mean levels (the same for males and females) were between 11% and 13% while yearly estimates varied from a low of 2% to a high of 35%. Both the survivorship and transition probability reported by Ens et al. (1995) are likely too high for the entire population of subadults because younger subadults often do not show up on the breeding grounds (Goss-Custard et al. 1982). I used a transition probability from subadult to adult of 0.15 (SD 0.13) (Table 1) which is between the estimates given by Safriel et al. (1984) and Ens et al. (1995). There was insufficient information in the literature to estimate and remove sampling variance from the published transition rates.

Estimates of juvenile survival in European Oystercatchers are quite variable. Goss-Custard et al. (1982) found that about 88% of juveniles survive their first fall and winter.

Other studies, however, have estimated juvenile survival at 64% (Boyd 1962) and 60% (Harris 1967). Kersten and Brenninkmeijer (1995) estimated average juvenile survival at only 40% based on return rates to natal breeding sites; return rates for cohorts varied from 10% to 68% depending on the severity of their first winter. Without the one extreme winter where only 10% of the cohort returned, the average return rate was 50% (Kersten and Brenninkmeijer 1995). Published estimates of variability in juvenile survival in Eurasian Oystercatchers were not amenable to partitioning so it is unclear how much of the variation was due to sampling error. For the baseline model I used an estimate of 0.70 (SD 0.11) average juvenile survival (midpoint of the high and low estimates described above). The largest concentrations of wintering American Oystercatchers are in areas of relatively mild winter weather (South Carolina, Virginia, and Florida) (Nol et al. 2000, Brown et al. 2005) and, thus, may not be subject to the extremes described for the European Oystercatcher.

Fecundity was defined as the number of female chicks per female per year, or one half of the number of chicks produced per pair per year, assuming an even sex ratio in the chicks. The sex ratio of American Oystercatcher hatchlings is unknown, but Eurasian Oystercatchers produce equal numbers of males and females, so this assumption is reasonable (Heg et al. 2000). Baseline fecundity was estimated from 912 breeding pairs monitored in North Carolina between 1998 and 2007. I assumed an even sex ratio in fledged chicks (N=266), so the mean rate of female chicks fledged per female adult per year was 0.146 chicks per pair. Attempts to separate temporal variance in fecundity from sampling variance (Gould and Nichols 1998, White et al. 2001 Akçakaya 2002), returned negative results, indicating little temporal variation or that the sampling variation was too large to

estimate temporal variation (Gould and Nichols 1998). As a result, our estimates of fecundity in the model did not include a measure of temporal variability.

After developing a baseline model, I created a set of alternative population matrices with elevated mean fecundity to simulate the effect of hurricane events. Hurricanes can have a powerful effect on oystercatcher reproductive success through predator reduction and habitat creation. Nest survival increased by as much as 400% in the year after a hurricane on Cape Lookout National Seashore, but returned to the pre-hurricane baseline rate within three years (Schulte and Simons in rev.). From 1886-2004 the North Carolina coast was struck by an average of 0.28 hurricanes per year (State Climate Office of North Carolina 2006). A given hurricane will not affect all areas of the coast equally, so the probability of any single location experiencing a hurricane will be lower than the cumulative probability for the region. Jagger et al. (2001) used a maximum likelihood estimator to model hurricane strike probabilities for coastal counties in the southeastern United States. Strike probabilities for North Carolina counties ranged from 0.248 (one hurricane every 4 years - Dare county) to 0.044 (one hurricane every 20 years - Onslow county). The hurricane matrix for our simulations was selected based on a set probability of either 0.1 (10 year hurricane event) or 0.0667 (15 year hurricane event). I used a mid-range and an infrequent value in our simulations because the model represents effects along the entire coast of North Carolina and few locations had strike probabilities higher than once every ten years. Initial post-hurricane fecundity was set at 0.553 female chicks per female based on data from Cape Lookout National Seashore following Hurricane Isabel (Schulte and Simons, in review). I simulated the return to pre-hurricane fecundity by using 0.35 female chicks per female for the first year



after the initial increase and 0.25 for the second year. For each year of the model simulation, the set of hurricane matrices was selected with a probability of 0.1 to simulate a 1 in 10 chance of a hurricane impact or 0.0667 to simulate a 1 in 15 chance of a hurricane impact.

I compared the outcomes from each parameter set using the population growth rate ( $\lambda$ ) and the projected population change over time. Each model set (baseline, 10 year hurricanes, 15 year hurricanes) was projected 10000 times over 50 years, twice the average oystercatcher lifespan (Safriel et al. 1984). Because of the uncertainty in population projections when stochasticity is included in parameter estimates (Akçakaya et al. 1999), I also used probabilistic results (risk of decline) to compare the models. I modeled the probability of a 50% decline during the 50 year simulation. A 50% decline is a benchmark often used in conservation planning to identify high priority species or populations (Akçakaya and Sjögren-Gulve 2000).

### Results:

The oystercatcher population declined under the baseline model (Table 2). The finite rate of population growth ( $\lambda$ ) for the baseline model was 0.986 (SD 0.007) with a mean population decline of 632 individuals (SD 216.2, 49% decline) over 50 years. In 62.5% of the simulations the population decreased by at least 50% during the 50 year period (Table 2). When I increased the hurricane probability to 0.0667, or a 1 in 15 chance of a hurricane strike,  $\lambda$  increased to 1.0029 (SD 0.011) with a mean population increase of 192 individuals (SD 895.13, 15.3% increase). The population declined by at least 50% in 16% of the simulations. When hurricane frequency increased to 1 in 10 years,  $\lambda$  increased to 1.0099 (SD

0.012) with a mean population growth of 802 individuals (SD 1351.4, 63.9% increase) over 50 years. The population declined by at least 50% in only 7.6% of the simulations.

In the absence of a hurricane effect or a change in adult survival, an increase in average annual fecundity could prevent population decline. Our model projects a stable population ( $\lambda = 1.000$ ) when baseline fecundity increased from our empirical estimate of 0.146 to 0.195 female chicks per female (0.39 chicks/pair).

As expected for a long lived species with a low reproductive rate, the proportional sensitivity of  $\lambda$  to adult survival was much higher than to any other parameter (Table 3). Small changes in adult survival can have large effects on the trajectory of a population.

#### Discussion:

Barrier island systems are in a constant state of low-level change. Wind and currents build and erode beaches while pioneering grasses colonize sandflats and are washed out by tides and storms. Hurricanes are a powerful force in the coastal zone and have the capacity to reshape barrier island ecosystems overnight. A strong hurricane can fully over-wash a low lying barrier island chain, reset succession, flatten dunes, and alter or eliminate meso-fauna communities.

Hurricane frequency and intensity is expected to increase in coming decades as ocean temperatures rise as a result of multi-decadal oscillations in the North Atlantic and increased atmospheric greenhouse gases (Goldenberg et al. 2001, Emanuel 2005 Webster et al. 2006). The frequency of hurricanes and associated high productivity years can have a large effect on the trajectory of Oystercatcher populations. In the absence of hurricane events our model

projects a rapid decline for American Oystercatchers in North Carolina over 50 years. A hurricane probability of 0.067 or a 1 in 15 chance of hurricane strike each year was enough to prevent population decline, while a probability of 0.1 or a 1 in 10 chance led to a rapidly increasing population. These projections are not intended to be absolute predictors for the oystercatcher population in North Carolina. I did not include estimates of variability on fecundity estimates because our empirical estimate of variance in fecundity was fully attributable to sampling variation (Gould and Nichols 1998). This may have caused us to underestimate the risk of decline if I was not able to capture the true process variation. One weakness of our model is the use of juvenile and subadult survival and transition rates from European Oystercatchers. I recognize that American Oystercatchers may have different survival rates and opportunities to establish breeding territories. Ongoing studies are in place to address these missing pieces, but given the relative sensitivity of population growth to adult survival over subadult survival and transition I feel that this model provides a reasonable representation of the response of Oystercatcher population to stochastic events. Estimates of transition rates and true survival are always problematic because mortality is confounded with emigration unless the study area encompasses the entire range of the marked individuals. Rather, if we accept that model parameters are close to their true values, our projections illustrate the relative effects of variable hurricane frequencies on American Oystercatcher populations. Population modeling is a useful endeavor if it provides a better understanding of the likely response of a population to changing parameters, and helps set priorities for future data collection efforts (Boyce 1992; Groom and Pascual 1997).

American Oystercatchers appear to have evolved a life history strategy shaped by periodic disturbance of their nesting habitats. Adaptations to some types of disturbance are well understood. Fire is a common source of regular disturbance throughout much of North America. A wide array of plant species are adapted to or even dependant on fire disturbance and these adaptations influence other parts of the ecosystem. Kirtland's Warblers, for example, nest exclusively in young jack pines, a fire dependant species (Mayfield 1992). In the Southeast United States hurricanes are a major source of disturbance, resetting barrier island succession and altering coastlines. The model presented in this paper was based on the observed effects from a category 2 hurricane (Hurricane Isabel) with winds around 166 kph and a storm surge from 2-5 meters. In the Northeast United States and the North and West coasts of Europe strong winter storms play a similar role in shaping coastal habitats. The exact location and strength of strong storms may be unpredictable and infrequent , but Oystercatchers are a long lived species and may experience the effects of a hurricane or other strong storm several times over their lifespan. Oystercatchers appear to exploit this type of disturbance through increased recruitment of subadults into the breeding population and elevated nesting success for established breeders. Oystercatchers are delayed breeders, so there is typically a pool of non-breeders waiting for nesting territories (Nol and Humphrey 1994, van de Pol 2006, this study). When a strong storm creates new habitat non-breeders are poised to move in and begin nesting. Established nesting pairs will shift their nest location within a territory to take advantage of better habitat.

In addition to creating new nesting habitat, hurricane overwash fans provide access to foraging sites in marshes and mudflats on the back side of barrier islands. Oystercatchers are

unusual among shorebirds in that their chicks are semi-precocial and require feeding throughout the fledging period. Eurasian Oystercatchers fledge more chicks when they can bring their chicks directly to feeding sites and do not have to make foraging flights to and from the nesting area (Heg and van der Velde 2001). I observed a similar relationship on Cape Lookout where broods with direct access to soundside foraging areas experienced higher fledging rates (Schulte and Simons, in rev). Oystercatchers lay 2-3 eggs per clutch, but often only fledge one chick or fail completely. In most years the extra reproductive potential goes unrealized, but this strategy allows American Oystercatchers to take advantage of post-hurricane years with fewer predators, improved nesting habitat, and increased access to foraging areas (Schulte and Simons in rev). Long-lived seabird species like the black-legged kittiwake (*Rissa tridactyla*) employ a similar strategy. Kittiwakes lay 2-3 eggs, but typically only one chick survives to fledging (Gill et al. 2002). Thus, in most years the extra eggs are not useful, but they position the birds to double or triple their reproductive output in years of high food abundance.

Human actions can alter the effects of hurricanes on American Oystercatcher productivity. In our models I assumed that a hurricane strike resulted in higher survival of nests and chicks in subsequent years, similar to the phenomenon observed on Cape Lookout National Seashore from 2004 to 2006 (Schulte and Simons in prep). This increase resulted from reduced predator populations and improved or expanded habitat. Habitat management that mitigates these changes will also reduce or eliminate the positive effects of the storm. In 2004, new habitat created by Hurricane Isabel on Cape Hatteras National Seashore was quickly altered or eliminated as roads and artificial dunes were rebuilt. Oystercatcher

fecundity in these areas the following year was much lower than that of birds nesting in similar areas on Cape Lookout where the natural sand movement was unaltered and the island was heavily overwashed. Truly natural barrier islands with unaltered sand movement and inlet dynamics are increasingly rare. In North Carolina they are limited to the islands of Cape Lookout National Seashore and several islands managed by NC Audubon in the southeastern portion of the state. As traditional barrier island nesting habitat is lost to development, the habitat quality on remaining sites becomes more important. In the face of this habitat compression, more frequent hurricanes or management practices that simulate hurricane disturbance may be critical to maintaining viable populations of American Oystercatchers in the Southeastern United States.

Actions that affect adult survival will have the greatest influence on population trends, but this is generally the least tractable parameter to manage. American Oystercatchers winter in flocks along the Atlantic and Gulf coasts, which places them at risk from local catastrophic events such as oil spills or loss of roost sites. Habitat protection and reducing pollution of food sources may prevent declines in adult survival. Fecundity, and to a lesser extent, subadult to adult transition rates are more amenable to management actions. Fecundity is reduced by nest predation, disturbance, and spring storms (Nol and Humphrey 1994, Davis et al. 2001, McGowan et al. 2005, Sabine et al. 2006). It may be possible to mimic or extend the effect of hurricanes by managing populations of nest predators, particularly non-native and artificially abundant mammalian mesocarnivores.

Predictions about the ecological effects of climate change usually focus on large scale patterns of atmospheric change, or negative impacts on a species or ecosystem. Estimates of

global temperature increases over the next century range from 1.8 to 4.0 degrees centigrade (IPCC 2007), and the warming trend is already affecting many species. The loss of arctic sea ice threatens polar bear (*Ursus maritimus*) populations (Derocher et al. 2004). Amphibian populations worldwide have declined severely as a result of the chytrid fungus (*Batrachochytrium dendrobatidis*) which is more virulent at higher temperatures (Bosch et al. 2007). This focus is important in the context of promoting human welfare and conserving biodiversity. At the same time, it is important to recognize that climate change will produce both winners and losers at the species, community, and ecosystem levels. American Oystercatchers appear to have a life history adapted to take advantage of periodic severe disturbance events caused by hurricanes. An increase in the frequency and intensity of tropical cyclones should benefit American Oystercatchers and other barrier island nesters because storm overwash improves habitat and reduces predator populations. The long-term future of the American Oystercatcher is by no means certain because some climate change effects such as sea level rise may result in a net loss of suitable habitat. Nevertheless, the relationship between hurricane disturbance and oystercatcher population growth provides evidence for at least one positive effect of climate change on this species of conservation concern.

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Table 1.3 Input parameters for baseline and alternate parameter sets. Parameter estimates are reported as mean values with standard deviations in parentheses. Initial Population = 679 adults; 447 subadults; 129 juveniles.

Model	Fecundity (F)	Juvenile survival (S <sub>j</sub> )	Second year survival (S <sub>s1</sub> )	Subadult survival w/o transition (S <sub>s2</sub> )	Subadult transition to adult (T <sub>s2a</sub> )	Adult survival (S <sub>a</sub> )
Baseline	0.146 <sup>1</sup>	0.70 <sup>2</sup> (0.11)	0.92 <sup>3</sup> (0.030)	0.77 <sup>3</sup> (0.030)	0.15 <sup>3</sup> (0.13)	0.92 <sup>4</sup> (0.030)
Post –Hurricane	0.553 <sup>1</sup>	0.70 (0.11)	0.92 (0.030)	0.77 (0.030)	0.15 (0.13)	0.92 (0.030)
Post Hurricane +1 year	0.35 <sup>1</sup>	0.70 (0.11)	0.92 (0.030)	0.77 (0.030)	0.15 (0.13)	0.92 (0.030)
Post Hurricane +2 years	0.25 <sup>1</sup>	0.70 (0.11)	0.92 (0.030)	0.77 (0.030)	0.15 (0.13)	0.92 (0.030)

Parameter data sources:

- 1: Breeding success data from Cape Lookout and Cape Hatteras National Seashore. 1998-2007.
- 2: Literature sources on juvenile survival rates of the Eurasian Oystercatcher (*Haematopus ostralegus*). Goss-Custard et al. (1982), Kersten and Brenninkmeijer (1995), Boyd (1962), Harris (1967).
- 3: Literature sources on subadult survival and transition rates of the Eurasian Oystercatcher (*Haematopus ostralegus*). Ens et al. (1995), Heg et al. (2000), van de Pol et al. (2007), Safriel et al. (1984), Goss-Custard et al. (1982), and Durell and Goss-Custard (1996).
- 4: Mark-recapture data from Cape Lookout and Cape Hatteras National Seashore. 2001-2007.

Table 2.3. Results of American Oystercatcher population model runs. Risk of decline is defined as the probability of the population declining by at least 50% during the 50 years simulation to fewer than 628 individuals.

Model	Risk of 50% decline	$\lambda$ , finite rate of increase	Population change over 50 years
Baseline	0.625	0.9860	-632 (SD 216.16, -49.7%)
15 year hurricane event	0.160	1.0029	+192 (SD 895.1, 15.3%)
10 year hurricane event	0.076	1.0099	+803 (SD 1351.4, +63.9%)

Table 3.3. Elasticity values for each element of the population matrix. S<sub>j</sub>: Juvenile survival.

S<sub>s1</sub>: Subadult (2) survival without transition to adult. S<sub>s2</sub>: Subadult (2) survival without

transition to adult. T<sub>s2</sub>: Subadult survival with transition to adult. S<sub>a</sub>: Adult survival. F:

Fecundity

0	0	(F*TS <sub>2</sub> ) = 0.0128	(F*S <sub>a</sub> ) = 0.07525
(S <sub>j</sub> ) = 0.088129	0	0	0
0	(S <sub>s1</sub> ) = 0.088129	(S <sub>s2</sub> ) = 0.220707	0
0	0	(TS <sub>2</sub> ) = 0.075249	(S <sub>a</sub> ) = 0.439657



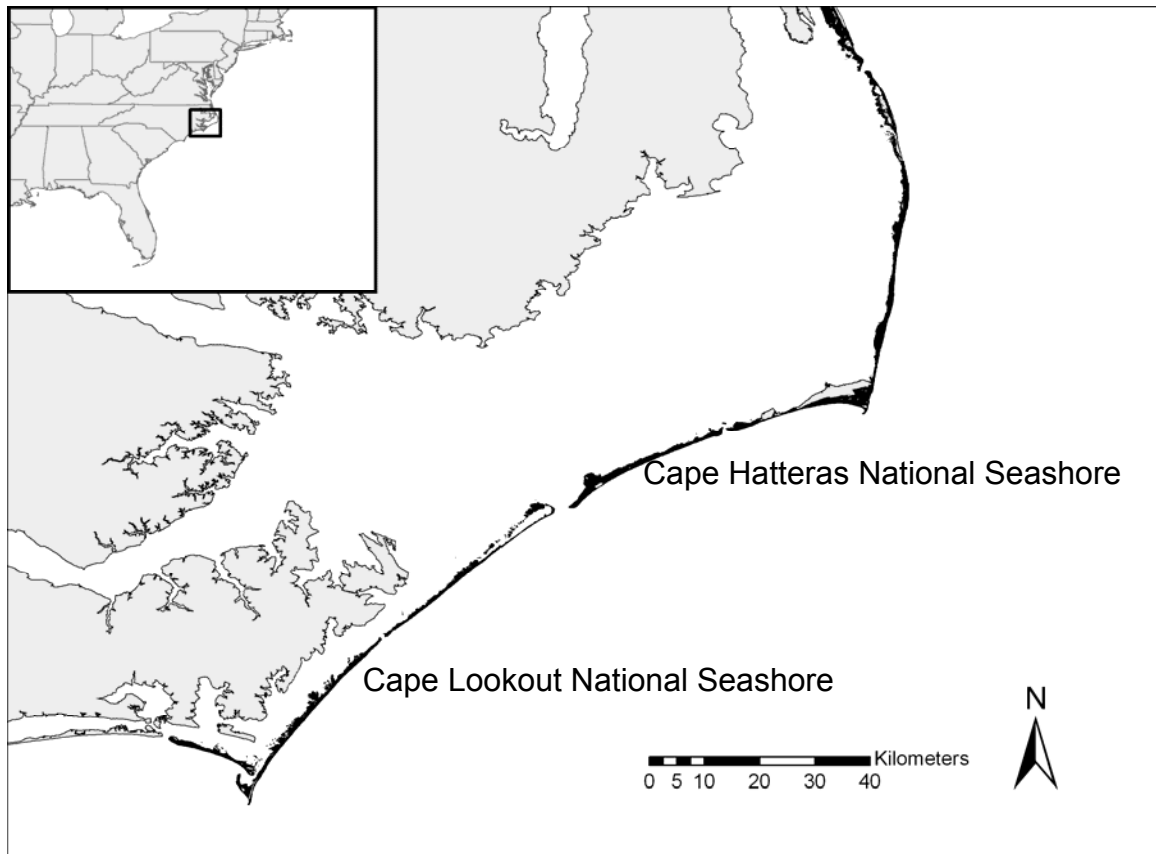


Figure 1.3. Study sites in North Carolina.

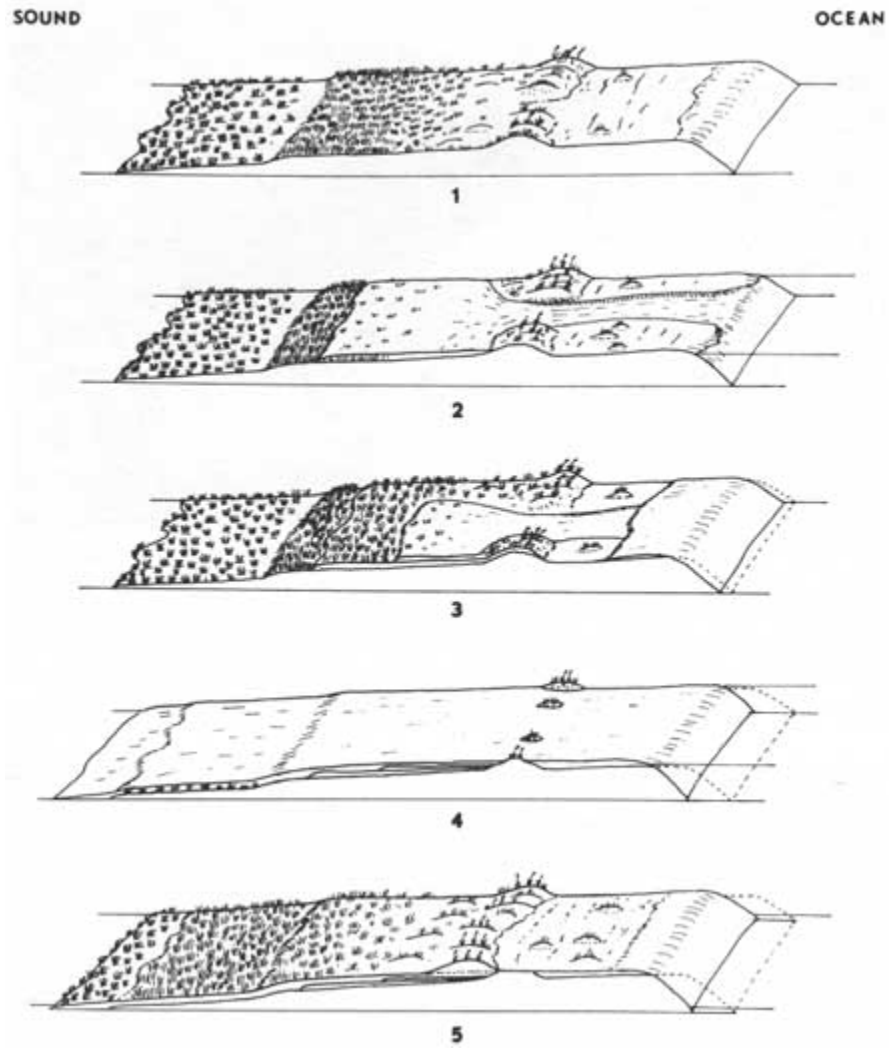


Figure 2.3 A diagram of the processes of overwash and recovery on a natural barrier island in North Carolina (from Godfrey 1970).

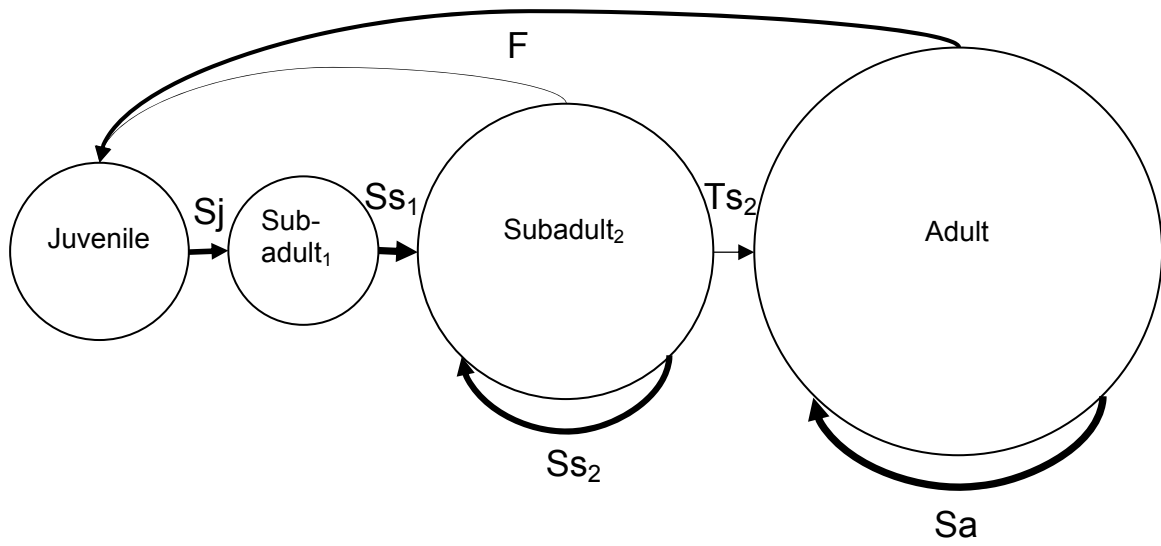


Figure 3.3. A conceptual stage-based model diagram of an American Oystercatcher population. The size of each node represents the proportion of the population in that stage. Arrow width corresponds to parameter values.

## **Chapter 4**

### **Migration and fidelity: American Oystercatcher movement patterns in North America**

Abstract:

I quantified Oystercatcher migration patterns and site fidelity, through an analysis of eight years of range-wide mark-recapture data. I also identified weakness in the current largely ad hoc approach to cooperative mark-resight work and outlined steps to a more rigorous mark-recapture methodology that will yield long-term, statistically valid estimates of population and movement parameters. Members of the American Oystercatcher working group banded 1424 Oystercatchers on the East Coast from Florida to Massachusetts between 2001 and 2008, and resighted 6127 color-marked birds during the same period. Migration strategy varied with latitude. The probability of migration decreased from North to South. Virtually all Oystercatchers breeding in New England and Long Island migrate in the fall. Northern breeders tended to leapfrog over mid-Atlantic wintering sites and concentrate in southern wintering sites, notably the west coast of Florida. Forty-eight percent of Oystercatchers breeding in Virginia did not migrate. Breeding Oystercatchers from South Carolina to Florida moved locally during the winter but did not migrate. Oystercatchers display strong site fidelity to both breeding and wintering sites. The rate of fidelity to breeding territories in North Carolina was 89%. Winter home range size was variable but relatively small (1.77km – 6.67km), and annual fidelity to winter range was 87%. The current ad-hoc approach to range-wide mark-recapture yields interesting results, but cannot support a rigorous analysis of movement and survival rates. Coordinated ongoing breeding season resight surveys combined with periodic winter surveys would allow us to track spatial and temporal changes in survival, recruitment, reproductive success, and migratory patterns.

## Introduction:

Movement patterns and connectivity in migratory birds influence how events in one season or location will affect populations at other stages of the annual cycle. If a large proportion of a given breeding population migrates to a single wintering area the viability of the population will be heavily influenced by threats at either site (Myers et al. 1987).

Conversely, breeding populations that disperse across multiple wintering areas will be less affected by events at any single wintering location (Webster et al. 2002, Kelly et al. 2002).

Comprehensive conservation strategies for at-risk species should therefore include an understanding of migratory connectivity patterns. In order to predict the effects of habitat loss, environmental damage, or conservation actions on population trajectory we need to know how those events will affect the birds throughout their annual cycle (Sillett et al. 2000, Rubenstein and Hobson 2004, Webster and Marra, 2005). By its very nature, migratory connectivity is difficult to study because of the challenges involved in following individual birds throughout the year.

American Oystercatchers (*Haematopus palliatus*) are large, conspicuous, long lived shorebirds that are restricted to a rapidly changing coastal environment. Their populations are currently the subject of a broad and coordinated research and monitoring efforts along the Atlantic and Gulf Coasts of the United States (American Oystercatcher Working Group 2011). All of these factors combine to make this species an ideal subject for investigating questions about movement and connectivity. Currently, our primary tool for studying American Oystercatcher demographics and movement is resighting birds banded with individually numbered leg bands. Geolocators are also being applied in some studies of

American Oystercatcher movement and may deepen our understanding of movement patterns, site fidelity, and dispersal. Additional techniques such as stable isotope analysis, and smaller satellite transmitters, are advancing our understanding of migration strategies, pathways and connectivity for an array of bird species (Marra et al. 1998, Hobson 1999, Croxall et al. 2005, Stuchbury et al. 2009, Shaffer et al. 2005) and may also inform future oystercatcher research and conservation efforts.

The migratory strategies of closely-related European Oystercatcher (*Haematopus ostralagus*) populations vary considerably across the range of the species. Northern breeders have the advantage of high productivity breeding sites and limited competition, but they must face the hazards of migration and strong competition for winter territories with Southern breeders (Hulscher et al. 1996). American Oystercatchers may experience similar constraints and tradeoffs. For instance, breeding populations in the southern portion of the range may move very short distances or even remain on breeding territories year-round, while movements of northern birds may produce different patterns of connectivity. For this analysis I used data from study sites in six Atlantic Coast states to examine patterns of dispersal and site fidelity.

Site fidelity, or the propensity to return to the same location in subsequent years, is characteristic of many bird species (Greenwood 1980, Greenwood and Harvey 1982, Holmes and Sherry 1992, Haas 1998). Returning to a previously inhabited location must generally confer a strong selective advantage for the behavior to persist in populations. Knowledge of food resources, the predator community, nesting sites, and neighbors may all be advantages for birds returning to a breeding or wintering site. Offsetting these advantages is the

potential to find better habitat elsewhere. Many studies have shown correlations between breeding success and age with the degree of site fidelity (Harvey et al. 1979, Oring and Lank 1982, Gratto et al. 1985, Newton and Marquiss 1982). Exceptions include Piping Plovers (*Charadrius melodus*) (Haig and Oring 1988) in which breeding success was not correlated with site fidelity, and Least Terns (*Sterna antillarum*) (Atwood and Massey 1988) where neither age nor breeding success were strong influences on site fidelity.. Switzer (1993) proposed a dynamic model which predicted that site fidelity should be inversely related to heterogeneity in territory quality, and positively related to the cost of changing territories, age, and probability of mortality in the habitat.

Patterns of movement and site fidelity are well understood for the European Oystercatcher (Goss-Custard et al. 1982, Ens et al., 1995, Heg et al., 2000, van de Pol et al. 2007), but estimates are generally lacking for the American Oystercatcher. Breeding site fidelity in Eurasian Oystercatchers is generally high, but is influenced by age, population density, and breeding success (Harris 1967, Ens et al. 1995). Ens et al. (1995) modeled the probability of changing status between breeding and non-breeding and between high vs low quality territories as Markovian processes. Birds in high quality territories were more likely to fledge young and more likely to retain the territory the following year. The probability of retaining a territory also increased with the number of seasons an individual was resident on a territory. Subadult birds often waited years for high quality territories rather than settling in more readily available low quality sites. Seniority was also the primary factor in establishing dominance on winter foraging territories (Heg et al. 2000).



American Oystercatchers are thought to have fairly high breeding site fidelity. Nol (1985) estimated the annual rate of return for breeding adults at 0.85. The rate of return for nesting Oystercatchers on the Outer Banks of North Carolina was estimated at 0.89 (SE 0.013) (Schulte and Simons in review). Neither of these studies estimated movement rates between territories in subsequent years.

An initial study of banded Oystercatcher chicks in North Carolina suggested that American Oystercatchers share the European Oystercatcher pattern of delayed recruitment (McGowan et al. 2005, Hockey et al. 1998). Sub-adult birds reach breeding age in their third summer, but many do not begin breeding until they are four to six years old. As in other long-lived species, demographic modeling of American Oystercatchers has demonstrated that the population growth rate is most sensitive to adult survival and the rate of recruitment to the breeding population. (Schulte and Simons in review, Safriel 1984).

In 1981, Nol (1985) initiated the first study of American Oystercatchers using individually marked birds. Her three year study on the Virginia coastal islands looked at the relative contribution of each sex to annual breeding efforts. This data set provided the first estimate of annual rates of return and adult survival. In 1999, researchers at North Carolina State University began trapping and color banding nesting Oystercatchers on the Outer Banks of North Carolina to estimate survival rates and understand patterns of movement and dispersal. Although limited in scope initially, this study grew to include all of the islands of the Outer Banks from Oregon Inlet to Beaufort Inlet, encompassing approximately 170 kilometers of coastline.

The formation of the American Oystercatcher Working Group in 2000 facilitated the exchange of ideas and methods among scientists and land managers interested in American Oystercatcher research and conservation. A better understanding of demographic rates and local and long-distance movement was a key research priority. In the winter of 2001 color banding projects were initiated in South Carolina and Georgia. Unlike previous efforts, these projects focused on capturing wintering flocks. Cohorts banded during the winter were primarily tracked to document survival, foraging patterns, and movement during the non-breeding season (Sanders et al. 2004, Peters and Otis 2005). In coordination with the working group, additional Oystercatcher research and management projects were subsequently initiated in Massachusetts, New Jersey, Delaware, Maryland, Virginia, Florida, Louisiana, and Texas. There is now at least one active American Oystercatcher management and/or research project in every Atlantic state and all of the Gulf Coast state except Mississippi and Alabama. Mark-resight methods and effort vary among studies, which currently limits the use of rigorous analytical methods to explore transition probabilities among sites and other demographic parameters.

In this paper I (1) quantify the cooperative mark-resight effort and describe apparent Oystercatcher migratory patterns, (2) estimate rates of breeding and wintering site fidelity, and (3) outline the steps needed to move from the existing ad hoc approach to a more rigorous methodology that will yield long-term, statistically valid estimates of population and movement parameters.

## Methods:

### *Mark-resight*

Members of the working group banded 1424 Oystercatchers between 2001 and 2008, and resighted 6127 color-marked birds during the same period (Table 1). Oystercatchers were captured with a variety of techniques, including cannon nets, noose carpets (McGowan et al. 2005), Whoosh nets (Doherty 2009), bow traps, and box traps. Resights came from a variety of sources ranging from comprehensive resight surveys by experienced observers to independent observations reported by members of the public. All resights were subject to quality control and verification by reviewing photographs of the birds where possible and comparing reports against banding records and previous resightings. Unusual records were flagged for confirmation. Organized banding and resight efforts were coordinated by members of the American Oystercatcher Working Group. Researchers used a common banding protocol where each state was assigned a band color and individual birds were identified by unique two-character codes engraved on the bands. Each bird was banded with an identical band on each leg to maximize the resighting probability and guard against band loss. Banding and resight records were compiled in a single database at North Carolina State University.

### *Breeding site fidelity*

I used 89 individually marked birds and eight years of mark-resight data from the Outer Banks of North Carolina to model the probability of an adult Oystercatcher returning to the same breeding territory or moving to a new territory in a subsequent year. I used a two state model with states defined as “initial territory” or “new territory”. This model was

parameterized with survival, spatial transition, and sighting probabilities defined as:  $\Phi_{i,j,k}$  = probability that a bird alive and present in state  $j$  during year  $i$  survives and is present in state  $k$  during year  $i + 1$ ;  $P_{i,j}$  = Probability that a bird present in state  $j$  during year  $i$  is sighted during that period. I followed Joe and Pollock (2002) and used the multi-state recaptures only procedure in Program Mark (White 2003) to separate survival and movement rates. Using this method, I assume that survival from time  $i$  to  $i+1$  does not depend on state at time  $i+1$ . In this case  $\phi_i^{rs} = S_i^r \psi^{rs}$  where  $\psi^{rs}$  is the conditional probability that an animal in state  $r$  at time  $i$  is in state  $s$  at time  $i+1$ , given that the animal is alive at  $i+1$ . ( $\psi^{rr} + \psi^{rs} = 1$ ).

Oystercatchers on the Outer Banks defended territories with a radius of up to 1.5 km, so a bird was treated as remaining in the same territory if it nested within 1.5km of the previous year's nest.

#### *Wintering site fidelity*

Estimating winter site fidelity was somewhat more difficult than estimating fidelity to a breeding territory. Within a season or even a single day, wintering Oystercatchers move between multiple roost sites and foraging areas depending on wind, tides and disturbance (Figure 1).

Winter home ranges could serve as the basis for estimating annual movement rates, but as I described earlier, gaps in spatial and temporal survey coverage at larger scales severely limited our ability to conduct this type of analysis. Therefore, I instead selected a subset of banded cohorts from four wintering areas to compare observed movement distances within seasons and between years. The subsets were chosen based on locations with comprehensive survey efforts for at least three years in a row. I selected Beaufort, North

Carolina, Bulls Bay, South Carolina, Altamaha River delta, Georgia, and Cedar Key, Florida as the focal sites. I measured the average distance between resight locations for each bird in each cohort within season and between years.

## Results:

### *Migration*

Migration strategies varied with latitude. One hundred and forty-seven Oystercatchers were banded in Massachusetts during the breeding seasons between 2003 and 2008. Seventy-six were subsequently observed on winter territories. Massachusetts breeding Oystercatchers were sighted in the winter from New York to Florida, but there were two regions where sightings were concentrated. 41% of the resighted birds were located on the Northwest Florida coast between Apalachicola and Tampa Bay, which contains approximately 10% of the total wintering population of Oystercatchers in the United States (Brown et al. 2005). The majority of these sightings occurred in the vicinity of the Cedar Key islands. Of the resighted Oystercatchers from Massachusetts, 28% were found in South Carolina, which hosts approximately 3300 Oystercatchers during the winter (Brown et al 2005), or 30% of the total population. The remaining individuals were distributed among the rest of the Atlantic states, with no single area containing more than 9% of the resighted birds. None of the birds banded in Massachusetts remained in the state during the winter. The longest recorded Oystercatcher migration was 2047km from Monomoy Island, MA to the 10,000 Islands region of Everglades National Park.

Oystercatchers nesting in New Jersey showed a similar pattern of migration. Seventy-nine Oystercatchers were banded during the breeding season in New Jersey between 2004 and 2008 and 62 were later resighted on winter territories. 35% of the resighted individuals were found on the Northwest coast of Florida, and 37% in South Carolina. Eight percent remained in New Jersey for the winter.

Oystercatchers on the Mid-Atlantic coast exhibited a different strategy. Forty-eight percent of the birds banded in Virginia during the breeding season remained on the Virginia coast throughout the winter. The rest of the Virginia birds were distributed evenly among South Carolina, Georgia, and the West coast of Florida. A similar pattern was evident in North Carolina, where 32% remained in the state year-round, while the rest of the population migrated to South Carolina, Georgia, and Florida. Oystercatchers nesting in South Carolina and Georgia exhibited local movements during the non-breeding season but rarely moved more than 30km from their breeding territories. In Georgia adult Oystercatchers banded during the breeding season joined nearby non-breeding flocks during the winter, but were observed visiting their breeding territories throughout the non-breeding season (B. Winn, unpublished).

Band resight records from North Carolina and Massachusetts reveal that juvenile Oystercatchers remain with their parents for 4 to 12 weeks after fledging, then leave to join local pre-migration flocks. Birds in family groups exhibit highly individual migratory behavior. Juveniles from the same brood may leave at different times and join different flocks. In one instance, all three chicks from a single brood on Cape Lookout, NC successfully fledged, then dispersed over a period of 8 weeks. Two of the chicks joined a

post-breeding flock less than 3km from their natal territory. The third chick remained with the parents for 11 weeks post-fledging, then flew 65km to join a flock near Beaufort, NC where it overwintered. The adult birds remained on territory for two more weeks, before joining the nearby flock, and ultimately migrating to separate sites in South Carolina and Georgia. Both adult birds returned to the same nesting territory the following spring. In another instance a juvenile from Ocracoke, NC, flew 220km north to Virginia, spent the winter near Cape Charles, while a second chick from same family group flew 75km south to a wintering flock near Beaufort, SC. One adult stayed on territory throughout winter, the other flew nearly 800km south to overwinter in Northeast Florida. Dispersal of family units appears to be the rule rather than the exception. Of the 709 hatch-year Oystercatchers banded on this project, only two first year birds from the same brood were observed together in a winter flock.

The duration of the migration period also varied among individuals. One Oystercatcher was observed on Cape Cod, MA on September 8<sup>th</sup>, then resighted on September 10<sup>th</sup> near New Inlet, VA where it remained for the rest of the winter. Another bird migrated from Cape Cod, MA to Cape Romain, SC in a maximum of four days. Other individuals migrated to intermediate stopover sites, spending days or weeks before moving on to their final winter territory. Important migration staging and stopover sites include Monomoy NWR and Tern Island flats in Chatham, MA (Humphrey 1990, Schulte and Brown 2003), Stone Harbor, NJ (Brown et al. 2005), The Eastern Shore of Virginia (Wilke et al 2007, Brown et al. 2005.), Bull's Bay, SC (Sanders et al. 2004; Marsh and Wilkinson 1991), and the Altamaha River delta in Georgia (B. Winn unpublished, Brown et al. 2005).

### *Site Fidelity*

Nesting Oystercatchers showed a high degree of fidelity to nesting territories from year to year. Only 11% moved from the territory where they were initially banded to a new territory annually (Table 2). Average distance for territory transitions was 8.03km (SE 1.05). Oystercatchers that did move to a new territory tended to move back to their original territory in subsequent years at a higher rate (24% annually). Winter site fidelity was also strong. Average within season movements ranged from 1.77km to 6.67km. The maximum observed within-season movement was 38 kilometers. Average between season movements were very similar as most of the birds returned to the same winter roosts in subsequent years (Table 3). The largest observed between-season movement was 63 kilometers

### Discussion:

The cooperative mark recapture effort undertaken by the American Oystercatcher Working Group is extensive in scale and duration, and has yielded an array of valuable insights into movement, survival, and behavior. Thanks to this initiative we have a much better understanding of large-scale movement patterns. Previous surveys revealed the location of wintering concentrations (Brown et al. 2005, Sanders et al. 2004), but not the origin of the birds within the flocks. Understanding patterns of movement and connectivity across the range of the species is fascinating in its own right, but also reveals important information necessary for effective conservation. This study found that up to 40% of Oystercatchers in Massachusetts migrate to the Gulf coast for the winter, many of them congregating in the area of Cedar Key, FL. Given this high degree of connectivity between



Massachusetts and Florida, any environmental impact in the Gulf of Mexico would likely have a greater impact on Oystercatchers in the Northeast than those on the Southeast Atlantic coast. An effective conservation strategy for Oystercatchers in the Northeast should include partnerships with Florida organizations to ensure protection throughout the annual cycle. Conversely, birds from Virginia and North Carolina disperse more uniformly across the wintering range, thus potentially mitigating the effects of an impact to any one wintering site. Breeding birds in South Carolina, Georgia, and the Gulf of Mexico appear to be local or non-migrants and are therefore highly susceptible to events within their own range, but relatively unaffected by impacts elsewhere.

Although unusual for a shorebird, the partial migration strategy of American Oystercatchers is similar to the migration patterns of Snowy Plovers (Gorman and Haig 2002), Black Oystercatchers (Johnson et al. 2010), and Eurasian Oystercatchers (Salmonsén 1955) which are also temperate breeders and relatively short distance migrants. Partial migration is more common among landbirds, particularly in the southern hemisphere (Chan 2001, Webster and Marra 2005). Partial migration is often associated with leapfrog migration, where northern migrants winter farther south than residents or short distance migrants at intermediate latitudes (Welty 1982). Although American Oystercatchers are not classic leapfrog migrants, there is at least some element of this strategy among the more northern breeders as we observed with the relatively high connectivity between Massachusetts breeding sites and Florida wintering sites.

At the individual level, marking and resighting revealed previously unsuspected elements of migratory behavior. Prior to this initiative it was believed that Oystercatchers

migrated in family groups (Nol and Humphrey 1994). In fact, the decisions about when, where, and even if a bird should migrate appear to be made at the individual level, even for first year birds. The factors that affect a first year migrant's decision about when and where to migrate are not clear. These birds may join a staging flock and migrate with more experienced birds, or set off on their own until they find a suitable site. Genetic control of migration is unlikely as young birds from the same brood often migrate to different wintering sites. Once a bird selects a wintering site it shows a high degree of annual fidelity to that site. Winter site fidelity in Eurasian Oystercatchers is well documented (Goss-Custard et al. 1982), and appears to be a result of the dominance hierarchy that develops around winter feeding territories. Seniority equals dominance in this hierarchy so there is a premium on returning to the same site each year. In American Oystercatchers the winter home range appears to be variable in size, possibly as a result of the availability of local food and roosting resources, as well as predator abundance and human pressures.

Previous studies documented high fidelity to breeding territories in American Oystercatchers (Nol 1985, Tomkins 1954, Nol and Humphrey 1994), but did not quantify the frequency of territory switching or the dispersal distance when a territory was vacated. Our examination of breeding territory fidelity in a multi-state framework revealed that the annual return rates (given survival) are close to 90%. When a bird did leave a territory, fidelity to the new territory was only 75% and the remaining birds transitioned back to the original territory in most cases. These may be birds that attempted to move to a higher quality territory and failed to retain it, or birds that were temporarily driven out of their original territory. In the eight years of the study I never observed an Oystercatcher moving among

more than two territories. These transition rates assumed no permanent emigration from the study site. While the size of the study area (170 km of shoreline) relative to average movement rates does lend credibility to this assumption, it would be naïve to think this is completely accurate. Numerous small marsh and sand islands line the sounds of the Outer Banks of North Carolina, and breeding Oystercatchers were observed moving from beach habitat to sound-side islands on more than one occasion. Permanent emigration would lead us to underestimate survival and overestimate site fidelity.

Despite the wealth of information generated by the cooperative efforts of the American Oystercatcher Working Group, the current approach to surveying and resighting has a number of drawbacks which limit our ability to conduct more rigorous analyses. Mark-recapture studies were initially designed to address questions about local movement, survival, and behavior. Researchers reported sightings of marked birds to each other, but survey efforts were largely ad hoc and varied in scope and method among sites. Beginning in 2004 members of the working group agreed on a standard marking scheme and attempted to conduct more comprehensive winter resight surveys in their respective states. One intended outcome of these surveys was to provide the basis for a comprehensive analysis of large-scale movement and connectivity patterns in a multi-state modeling framework. Despite the best efforts of the group, significant difficulties arose that complicate this level of analysis. As resight efforts expanded and new observers took to the field, researchers found previously unsampled sites, particularly the sites on the west coast of Florida. In addition, several Atlantic coast states were not able to conduct full statewide surveys each year during the planned survey period. These circumstances combined to create several large areas

where banded birds had no opportunity to be resighted. Modeling methods have been developed to estimate transition rates to and from unobservable states and to account for permanent emigration (Burnham 1993, Nichols 1996, Kendall et al. 1997, Lindberg et al. 2001, Converse et al. 2009). These methods are based on Pollock's robust design (Pollock 1982) and incorporate multiple secondary samples within primary sampling periods. In the case of the Oystercatcher survey effort, logistical constraints prevented systematic subsampling in most sites and years. Even completing a single comprehensive survey was difficult or impossible in some years due to budget and personnel limitations.

The American Oystercatcher Working Group is ready to transition to a sustainable and standardized long-term mark-resight protocol. A well designed protocol will reduce uncertainty in the accuracy of the data and allow for more rigorous analysis of the demographic parameters needed to track populations. One solution is a revision of the original range-wide winter survey (Brown et al. 2005). Comprehensive and coordinated winter surveys carried out across the range of the species for at least four consecutive years would yield unprecedented data on survival of all age classes and substantial refinement in our understanding of movement rates and patterns. Key design elements would include coordinated surveys across the winter range conducted in a relatively short time window during the middle of winter when birds are most stable, and multiple surveys within this time window to allow for the estimation of resight probability and local movement rates. One advantage of this approach is that all of the Atlantic coast states have already conducted comprehensive winter surveys so we have a good understanding of the logistical requirements of such an undertaking. A significant challenge in implementing this approach

is that ongoing financial and logistical support that would be required, particularly in regions where boat access is crucial. Such an effort would be highly valuable and technically possible if the Working Group makes it a priority, but it is unlikely to be a sustainable, long-term strategy. A reduced version of this approach would be to visit and survey winter roost sites at least once during the non-breeding season, and/or reduce the frequency of surveys to three or five year cycles. Removing the requirement to conduct multiple surveys over a short time window each year would decrease the precision of survival estimates and make it difficult to estimate local movement rates. This type of winter survey would still permit qualitative analysis of migration patterns and allow observers to document and track changes in site use.

A non-exclusive alternative is to focus on marking and resighting birds during the breeding season. The population is spatially dispersed during the breeding season, but is also fairly stable and predictable, which allows for more flexibility in survey efforts. Annual breeding season resight surveys could be conducted in conjunction with ongoing monitoring and management efforts in many areas. Key design elements include comprehensive coverage so that any banded bird has the potential to be resighted (e.g. not excluding a particular area or nesting habitat), and completing the surveys after spring migration is complete and before birds begin to move to fall staging sites. Annual breeding season surveys would allow for the estimation of spatially and temporally explicit survival and immigration/emigration rates across the range of the species. This would be immensely valuable from a conservation standpoint as adult survival is the most important parameter driving oystercatcher population change (Schulte and Simons, in review). Understanding

how survival rates vary across the range of the species will yield insights into differences in population trajectories and the relative contribution of each area to the growth or decline of the total population. Breeding season surveys would also allow for the estimation of recruitment rates and juvenile/subadult survival as young birds enter the breeding population. Implementing this type of survey during the already frenetic breeding season would likely require additional resources for many land managers and conservation organizations. Despite the inherent challenges, this type of breeding season resight survey is already underway at many sites on the Atlantic Coast and Gulf Coasts, which suggests that a fully comprehensive, coordinated approach is feasible given sufficient resources.

Over the long term, coordinated breeding season resight surveys combined with reduced intensity winter surveys would allow us to track survival, recruitment, reproductive success, and migratory patterns both spatially and temporally. Such an effort would advance our understanding of Oystercatcher biology, provide immense value for conservation, and serve as a model for the conservation of other species.

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Table 1.4 American Oystercatcher banding and resight records from 2001 – 2008.

Banding location	Age at banding			Resight records
	Juveniles	Second Year	After second year (adult)	
MA	35		112	781
VA	273	1	8	930
NJ	47	2	41	355
NC	230		136	1116
SC	105	21	249	2416
GA	19	12	133	529
<b>Total</b>	<b>709</b>	<b>36</b>	<b>679</b>	<b>6127</b>

Table 2.4 Movement matrix describing the annual probability of an adult Oystercatcher returning to a former territory or moving to a new territory. 2001-2008, N=89, Movement rates are conditional on survival. Standard errors in parentheses.

Initial State	New State	
	Original territory	New Territory
Original Territory	0.89 (0.02)	0.11 (0.02)
New Territory	0.24 (0.07)	0.76 (0.07)

Table 3.4 Average movement rates for banded cohorts of American Oystercatchers at four survey sites. Distances are in kilometers and represent the average distance between subsequent resights of individual birds. Standard errors in parentheses.

Site	Within Season	N	Between Years	N
Beaufort, NC	3.42 (2.20)	14	5.23 (2.84)	9
Bull's Bay, SC	1.77 (0.33)	35	2.03 (0.76)	21
Altamaha, GA	5.09 (1.37)	41	8.33 (1.41)	29
Cedar Key, FL	6.67 (1.11)	43	7.12 (2.05)	31



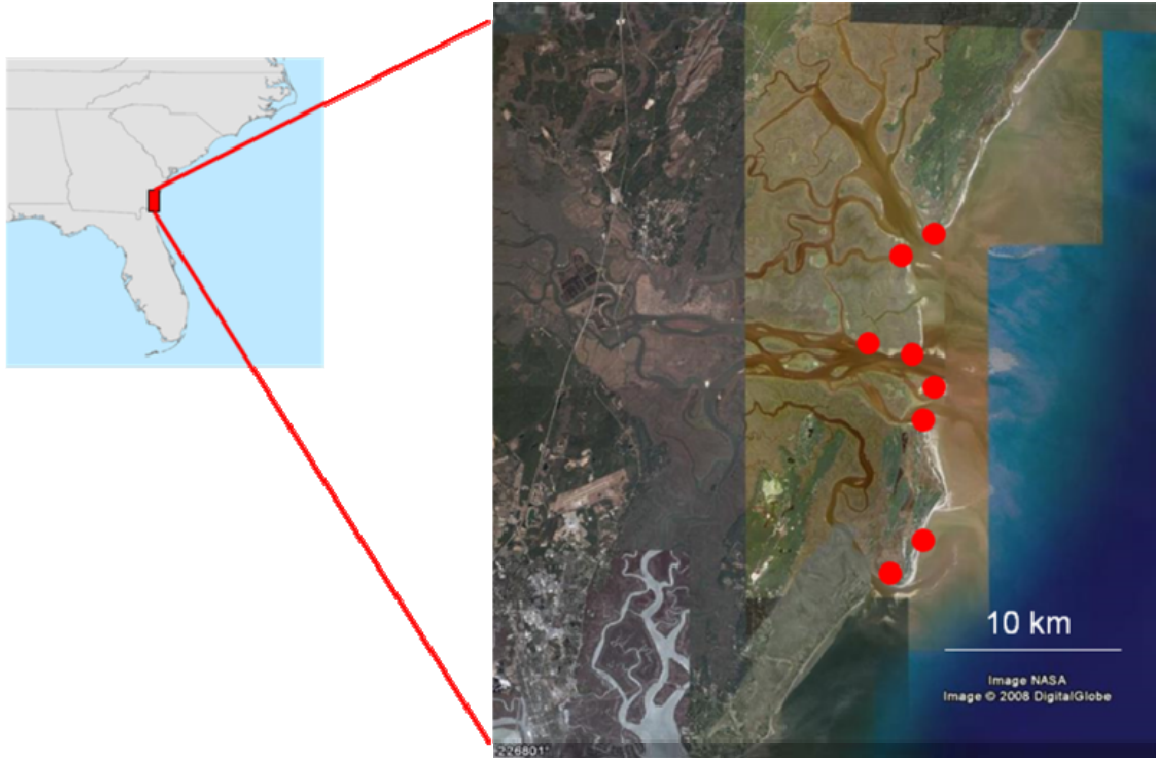


Figure 1.4 Winter resight locations for a banded American Oystercatcher near the Altamaha River Delta in Georgia (Winter 2005-2006).

## APPENDICES

Appendix A: American Oystercatcher productivity in North Carolina (1995-2008)

Year and Location	Breeding pairs	Nests	Nests hatched	Nest survival observed (SE)	Nest survival adjusted (SE)	Chicks fledged	Chick Survival (SE)	Chicks fledged/pair (SE)
<b>CAPE LOOKOUT</b>								
<b>North Core Banks</b>								
1998	38	72	5	0.069 (0.030)	NA	4	NA	0.105 (0.062)
1999	39	62	11	0.177 (0.049)	0.170 (0.042)	5	0.208 (0.083)	0.128 (0.061)
2000	29	36	7	0.194 (0.066)	0.248 (0.068)	1	0.059 (0.057)	0.034 (0.034)
2001	29	53	12	0.226 (0.057)	0.173 (0.049)	1	0.091 (0.061)	0.034 (0.034)
2002	23	46	4	0.087 (0.042)	0.084 (0.033)	5	0.455 (0.150)	0.217 (0.125)
2003	20	36	7	0.194 (0.066)	0.157 (0.053)	2	0.118 (0.078)	0.100 (0.069)
2004	21	25	20	0.800 (0.080)	0.772 (0.089)	31	0.608 (0.068)	1.476 (0.255)
2005	16	20	11	0.550 (0.111)	0.453 (0.120)	6	0.286 (0.099)	0.375 (0.155)
2006	14	18	8	0.444 (0.117)	0.399 (0.116)	5	0.263 (0.101)	0.357 (0.133)
2007	17	32	8	0.250 (0.077)	0.191 (0.065)	14	0.778 (0.098)	0.824 (0.261)
2008	14	22	4	0.182 (0.082)	0.248 (0.084)	3	0.429 (0.187)	0.214 (0.114)
Island	260	422	97	0.230 (0.020)	0.228 (0.021)	77	0.376 (0.035)	0.296 (0.043)
<b>Middle Core Banks</b>								
2004	5	5	4	0.800 (0.179)	NA	7	0.875 (0.117)	1.400 (0.510)
2005	7	9	5	0.556 (0.166)	0.511 (0.172)	9	0.643 (0.128)	1.286 (0.474)
2006	8	9	7	0.778 (0.139)	0.745 (0.155)	8	0.500 (0.125)	1.000 (0.267)
2007	11	11	7	0.636 (0.145)	0.570 (0.160)	10	0.833 (0.108)	0.909 (0.315)
2008	6	6	4	0.667 (0.192)	NA	7	0.875 (0.117)	1.167 (0.477)
Island	37	40	27	0.675 (0.074)	0.604 (0.096)	41	0.707 (0.060)	1.108 (0.168)
<b>Ophelia Banks</b>								
2007	2	3	2	0.667 (0.272)	NA	3	0.750 (0.217)	1.500 (0.500)
2008	2	2	1	0.500 (0.354)	NA	0	0.000 (0.000)	0.000 (0.000)

Island	4	5	3	0.600 (0.219)	NA	3	0.500 (0.204)	0.750 (0.479)
<b>South Core Banks</b>								
1995	20	36	12	0.333 (0.079)	NA	7	NA	0.350 (0.131)
1997	23	34	4	0.118 (0.055)	0.036 (0.022)	2	0.286 (0.171)	0.087 (0.060)
1998	20	26	7	0.269 (0.087)	0.135 (0.062)	3	0.214 (0.110)	0.150 (0.082)
1999	28	52	5	0.096 (0.041)	0.115 (0.036)	1	0.125 (0.117)	0.036 (0.036)
2000	25	38	18	0.474 (0.081)	0.303 (0.077)	6	0.120 (0.046)	0.240 (0.087)
2001	27	56	8	0.143 (0.047)	0.158 (0.042)	1	0.050 (0.049)	0.037 (0.036)
2002	23	43	4	0.093 (0.044)	0.061 (0.028)	1	0.143 (0.132)	0.043 (0.043)
2003	27	59	9	0.153 (0.047)	0.121 (0.036)	6	0.273 (0.095)	0.222 (0.096)
2004	20	33	13	0.394 (0.085)	0.279 (0.080)	6	0.231 (0.083)	0.300 (0.147)
2005	22	27	9	0.333 (0.091)	0.317 (0.086)	3	0.188 (0.098)	0.136 (0.068)
2006	19	31	6	0.194 (0.071)	0.203 (0.065)	10	0.769 (0.117)	0.526 (0.246)
2007	21	41	4	0.098 (0.046)	0.073 (0.032)	4	0.571 (0.187)	0.190 (0.131)
2008	24	44	5	0.114 (0.048)	0.087 (0.034)	5	0.625 (0.171)	0.208 (0.120)
Island	299	520	104	0.200 (0.018)	0.139 (0.014)	55	0.242 (0.030)	0.184 (0.027)
<b>Shackleford Banks</b>								
2003	7	10	1	0.100 (0.095)	NA	0	0.000 (0.000)	0.000 (0.000)
2004	6	8	1	0.125 (0.117)	NA	1	1.000 (0.000)	0.167 (0.408)
2005	9	10	1	0.100 (0.095)	NA	0	0.000 (0.000)	0.000 (0.000)
2006	9	11	1	0.091 (0.087)	0.071 (0.061)	1	1.000 (0.000)	0.111 (0.011)
2007	10	12	0	0.000 (0.000)	0.110 (0.088)	0	0.000 (0.000)	0.000 (0.000)
2008	11	17	3	0.176 (0.092)	0.059 (0.046)	0	0.000 (0.000)	0.000 (0.000)
Island	52	68	7	0.103 (0.037)	0.075 (0.035)	2	0.167 (0.108)	0.038 (0.027)
<b>CAPE HATTERAS</b>								
<b>Ocracoke Island</b>								
1999	15	17	7	0.412 (0.119)	0.321 (0.105)	2	0.182 (0.116)	0.133 (0.091)
2000	12	17	6	0.353 (0.116)	0.270 (0.107)	7	0.778 (0.139)	0.583 (0.260)
2001	13	15	11	0.733 (0.114)	0.624 (0.132)	12	0.600 (0.110)	0.923 (0.265)
2002	12	18	6	0.333 (0.111)	0.266 (0.102)	3	0.250 (0.125)	0.250 (0.131)

2003	8	12	4	0.333 (0.136)	0.255 (0.117)	1	0.250 (0.217)	0.125 (0.125)
2004	9	11	6	0.545 (0.150)	0.566 (0.144)	8	0.727 (0.134)	0.889 (0.309)
2005	5	10	3	0.300 (0.145)	0.295 (0.136)	1	0.167 (0.152)	0.200 (0.200)
2006	5	8	4	0.500 (0.177)	0.492 (0.202)	2	0.182 (0.116)	0.400 (0.400)
2007	5	12	3	0.250 (0.125)	0.102 (0.078)	1	0.250 (0.217)	0.200 (0.200)
2008	3	3	1	0.333 (0.272)	0.347 (0.260)	2	1.000 (0.000)	0.667 (0.667)
Island	87	135	51	0.415 (0.044)	0.341 (0.042)	39	0.433 (0.052)	0.448 (0.080)

#### Hatteras Island

1999	24	31	7	0.226 (0.075)	0.287 (0.087)	3	0.273 (0.134)	0.125 (0.069)
2000	23	29	10	0.345 (0.088)	0.270 (0.081)	2	0.087 (0.059)	0.087 (0.060)
2001	24	28	10	0.357 (0.091)	0.259 (0.083)	7	0.389 (0.115)	0.292 (0.112)
2002	17	25	3	0.120 (0.065)	0.030 (0.023)	4	0.800 (0.179)	0.235 (0.136)
2003	16	23	10	0.435 (0.103)	0.372 (0.106)	6	0.286 (0.099)	0.375 (0.155)
2004	15	18	13	0.722 (0.106)	0.706 (0.110)	9	0.360 (0.096)	0.600 (0.235)
2005	17	25	16	0.640 (0.096)	0.501 (0.110)	10	0.417 (0.101)	0.588 (0.196)
2006	14	19	11	0.579 (0.113)	0.525 (0.120)	6	0.316 (0.107)	0.429 (0.202)
2007	15	21	10	0.476 (0.109)	0.477 (0.102)	9	0.450 (0.111)	0.600 (0.235)
2008	15	20	9	0.450 (0.111)	0.565 (0.102)	11	0.611 (0.115)	0.733 (0.267)
Island	180	239	99	0.414 (0.032)	0.373 (0.032)	67	0.364 (0.035)	0.372 (0.052)

#### Bodie Island

1999	2	3	0	0.000 (0.030)	0.030 (0.035)	0	0.000 (0.000)	0.000 (0.000)
2000	2	3	0	0.000 (0.081)	0.081 (0.081)	0	0.000 (0.000)	0.000 (0.000)
2001	2	3	1	0.333 (0.272)	0.285 (0.253)	1	0.500 (0.354)	0.500 (0.500)
2002	2	5	1	0.200 (0.179)	0.138 (0.137)	2	1.000 (0.000)	1.000 (1.000)
2003	5	5	1	0.200 (0.179)	0.311 (0.182)	0	0.000 (0.000)	0.000 (0.000)
2004	3	6	0	0.000 (0.000)	0.091 (0.089)	0	0.000 (0.000)	0.000 (0.000)
2005	2	3	1	0.333 (0.272)	0.390 (0.260)	0	0.000 (0.000)	0.000 (0.000)

2006	2	2	1	0.500 (0.354)	0.400 (0.367)	0	0.000 (0.000)	0.000 (0.000)
2007	2	2	1	0.500 (0.354)	0.545 (0.331)	0	0.000 (0.000)	0.000 (0.000)
2008	3	5	2	0.400 (0.219)	0.361 (0.212)	2	0.100 (0.000)	0.667 (0.333)
Island	25	37	8	0.216 (0.068)	0.191 (0.053)	5	0.417 (0.142)	0.200 (0.100)
<b>Green Island</b>								
2004	2	3	2	0.667 (0.272)	NA	2	0.500 (0.250)	1.000 (1.000)
2005	2	3	2	0.667 (0.272)	NA	0	0.000 (0.000)	0.000 (0.000)
2006	2	2	2	1.000 (0.000)	NA	2	1.000 (0.000)	1.000 (0.000)
2007	2	2	1	0.500 (0.354)	NA	2	0.667 (0.272)	1.000 (1.000)
2008	2	4	1	0.150 (0.217)	NA	2	1.000 (0.000)	1.000 (1.000)
Island	10	14	8	0.571 (0.132)	NA	8	0.571 (0.132)	0.800 (0.293)
<b>CAPE FEAR REGION</b>								
<b>Cape Fear River Islands</b>								
2002	32	47	26	0.553 (0.073)	0.534 (0.073)	7	0.149 (0.052)	0.219 (0.074)
2003	34	50	15	0.300 (0.065)	0.367 (0.064)	7	0.333 (0.103)	0.206 (0.066)
Island	66	97	41	0.423 (0.050)	0.443 (0.049)	14	0.206 (0.049)	0.212 (0.049)
<b>Lea and Hutaff Islands</b>								
2003	16	16	11	0.688 (0.116)	0.617 (0.133)	9	0.391 (0.102)	0.563 (0.204)
<b>Total/mean</b>	<b>1036</b>	<b>1581</b>	<b>456</b>	<b>0.288 (0.011)</b>	<b>0.246 (0.011)</b>	<b>320</b>	<b>0.360 (0.016)</b>	<b>0.309 (0.020)</b>