EFFECTS OF URBANIZATION ON THE DISTRIBUTION AND

REPRODUCTIVE PERFORMANCE OF THE AMERICAN OYSTERCATCHER

(*HAEMATOPUS PALLIATUS PALLIATUS*) IN COASTAL NEW JERSEY

By

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A dissertation submitted to the

Graduate School-New Brunswick

Rutgers, The State University of New Jersey

In partial fulfillment of the requirements for the degree of

Doctor of Philosophy

Graduate Program in Ecology and Evolution

Written under the direction of Julie L. Lockwood

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October 2008

ABSTRACT OF THE DISSERTATION

Effects of Urbanization on the Distribution and Reproductive Performance of the

American Oystercatcher (*Haematopus palliatus palliatus*) in Coastal New Jersey

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Urbanization and associated human disturbance can affect American oystercatcher reproductive performance in direct and indirect ways. Nest success rates could be directly affected if human disturbance disrupts normal breeding behavior or leads to increased predation rates. Indirectly, reproductive performance could be reduced if distributional patterns are altered due to coastal development or disturbance on breeding grounds. This dissertation examines the influences that urbanization and human disturbance have on American oystercatcher reproductive rates and distribution in highly urbanized coastal ecosystems in New Jersey.

Human-induced effects on oystercatcher daily nest survival rates and overall reproductive performance were analyzed across a mosaic of habitats (Chapter 1). My results showed

that the principal factor negatively influencing daily survival rates of both clutches and broods was the presence of mammalian predators, not human disturbance. The nest success rate on predator-free islands (21%) was an order of magnitude greater than the rate reported on barrier islands (2%), which have high densities of predatory mammals. Thus, the direct effect of human disturbance on reproductive performance was trumped by the effect of mammalian predators.

The effect of urbanization and human disturbance on the local distribution of American oystercatchers was analyzed using species distribution modeling techniques including maximum entropy (MAXENT) modeling and classification and regression tree (CART) modeling. First, the distribution of oystercatchers in response to urbanization was analyzed using MAXENT (Chapter 2). This modeling technique provided a map of predicted habitat suitability that was used to locate oystercatcher populations. The results of validation surveys showed that the New Jersey oystercatcher population utilized alternative breeding habitats in very high concentrations. Next, the habitat suitability model was used as the starting point to develop CART models analyzing the effect of human disturbance on the local distribution on barrier beaches (Chapter 3). These models showed that high levels of human disturbance further influenced local oystercatcher distribution in New Jersey.

My dissertation shows that urbanization and associated human disturbance affect the distributional patterns of the American oystercatcher. Thus, these factors indirectly

affected reproductive performance by leading to the exclusion of oystercatchers from the most highly suitable breeding habitat.

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INTRODUCTION

Oystercatchers (family Haematopodidae) are habitat specialist shorebird species (order Charadriiformes) found along the coasts of every continent except Antarctica. There are 11 recognized species, split between two typical phenotypic forms: the pied forms which are found predominantly on sandy shorelines and the black forms which are found on rocky coasts. The American oystercatcher (*Haematopus palliatus*) is a pied oystercatcher that is found on sandy shorelines from South America to Nova Scotia along the Atlantic coast of Canada and to California on the Pacific coast of the United States. The species is split into five distinct sub-species: *H. palliatus dunfordi* in Argentina, *H. palliatus pitanay* in southwestern South America, *H. palliatus frazari* in western Mexico, *H. palliatus galapagensis* in the Galapagos Islands and *H. palliatus palliatus*, which is widely distributed from northern South America to Canada. The latter sub-species is the subject species of my research (hereafter referred to as the American oystercatcher).

My research examines the factors affecting the distribution and reproductive performance of American oystercatchers in coastal New Jersey. The traditional breeding habitat of the American oystercatcher historically was high elevation, sandy, isolated barrier island beach habitat along the coast of the United States (Hughes 1995; Nol 1994; Sibley 2001). Oystercatchers were previously extirpated from more northern parts of their historic breeding range, including New Jersey, as recently as 1900 due to market hunting and loss or alteration of critical breeding habitat. The species began to expand its range north

during the mid-1900s after hunting stopped (Davis et al. 2001), and the first documented record of oystercatchers breeding in New Jersey occurred on Ham Island in Ocean County in 1948 (Kramer 1948). Over the next several decades, the oystercatcher population in New Jersey increased as the species continued to expand its range northward along the Atlantic coast as it re-colonized parts of its former range. It was during this time that oystercatchers were first observed breeding in habitats other than traditional barrier island beach habitat, and it was hypothesized that this shift into alternative breeding habitat may have facilitated the recent range expansion (Humphrey 1990; Post & Raynor 1964).

By the 1960s oystercatchers were regular breeders on barrier island beaches in southern parts of New Jersey, returning first to traditional barrier island habitat (Post & Raynor 1964). The first documented record of an oystercatcher breeding in alternative habitat (saltmarsh) in New Jersey was in 1963 (Frohling 1965). Post and Raynor (1964) hypothesized that by 1962 the New Jersey oystercatcher population (on barrier beaches) may have been near the maximum that the region could support and that this was one of the principal factors leading to the species range expansion northward into the region.

The habitat shift into alternative breeding habitat such as saltmarsh, inlet and back-bay islands is not surprising due to anthropogenic changes to coastal ecosystems, which severely reduced the amount of traditional barrier beach habitat available for breeding. The most severe anthropogenic changes to coastal ecosystems in North America occurred between 1900 and 1950, coinciding with the period when oystercatchers began to re-

colonize former parts of their range. It was during the latter part of this period that coastal development in New Jersey increased dramatically. Prior to World War II, more than 90% of the barrier islands in the United States were still undeveloped (USFWS 2004), and coastal areas in New Jersey remained in a relatively natural state. By 1950, developed barrier island habitat in northeastern states such as New York and New Jersey reached 27% and 37%, respectively, and by 1974 increased an additional 10% in each state leaving little of the historic barrier island breeding habitat once available to beach-nesting shorebirds such as the American oystercatcher.

The intensive coastal development changed the landscape as roads and bridges were constructed connecting barrier islands to the mainland for the first time. This provided access to many islands that previously acted as refuges for oystercatchers and other beach-nesting avian species. The bridges led to the rapid development of these barrier islands as tourist destinations, and the landscape was quickly and severely altered. Intensive coastal development resulted in the complete loss of some potential breeding grounds on barrier beaches and the degradation of others. The dynamic nature of the barrier islands themselves was altered as beaches and inlets were stabilized with jetties in an attempt to stop the migration of sand (a natural and necessary process in the barrier island system) to protect human development interests. Access to foraging areas was cut off in many places as the shorelines on the back sides of the barrier islands were hardened with bulkheads or other man-made structures. Even where foraging areas remained intact, the historic food source for oystercatchers (American oysters *Crassostrea virginica*) was almost completely extirpated from our state's waters due to

over-harvesting and disease. Other bivalves such as ribbed mussels (*Geukensia demissa*) and blue mussels (*Mytilus edulis*) remained as alternative prey items, but these require different feeding strategies. Oystercatchers re-colonizing the severely altered coastline began to utilize alternative habitat to breed. Fortunately, oystercatchers show plasticity in their breeding and foraging ecology allowing them to change rapidly with their environment.

Although the American oystercatcher was known to breed in alternative habitats prior to the outset of my research in 2004, little was known as to the extent of use of these habitats or the population consequences of this habitat shift. Earlier studies documented the use of alternative habitats by oystercatchers; however, these studies did not explore the factors affecting the distributional change nor did they examine differential reproductive rates between habitat types (Lauro & Burger 1989; Nol 1989). To my knowledge, no extensive study examining the factors affecting the distribution of oystercatchers across a mosaic of habitats in urbanized coastal ecosystems had been conducted before my research. Additionally, until recently, little was known about the factors influencing the nest success of American oystercatchers or the effects of utilizing alternative breeding habitat on overall reproductive performance. Several recent studies examining the factors influencing nest success for American oystercatchers have shown that predation pressure and human disturbance contributed to lower reproductive rates or alteration of breeding behavior (McGowan & Simons 2006; McGowan et al. 2005; Sabine et al. 2006; Sabine et al. 2008). However, few studies have examined differential reproductive rates for oystercatchers between habitat types. McGowan et al. (2005)

found that reproductive rates varied between barrier beach and riverine island habitats and hypothesized that the latter habitat type may be acting as an ecological trap for oystercatchers. To my knowledge, this is the only study that has examined the effects of alternative habitat use by American oystercatchers to date. Much still needs to be understood about the effects of oystercatchers utilizing alternative habitats throughout the species' range taking into consideration the species' high annual variation in reproductive performance.

While we have begun to gain a better understanding of the breeding ecology of the American oystercatcher, much remains unknown. For example, we still do not have a clear understanding of the breeding distribution of the species. Winter surveys estimate that the population of the American oystercatcher is approximately 10,000 (Brown et al. 2005). However, breeding surveys have only identified approximately 3,000 breeding pairs, just over half of the overall estimated population (American Oystercatcher Working Group, unpublished data). Recent surveys have shown that many oystercatchers may have previously been overlooked in alternative habitats indicating that these areas may be more important than previously thought for the long-term viability of the population (Traut et al. 2006; Wilke et al. 2007). Understanding the current distribution of American oystercatchers across a mosaic of habitats and gaining a better estimate of the breeding population throughout the species' range are paramount in our attempts to conserve the species.

My research is the first attempt to explain the distribution of American oystercatchers in alternative breeding habitats in response to environmental and anthropogenic factors. Further, I provide one of the first studies analyzing the factors influencing oystercatcher reproductive performance in alternative habitats. I apply novel statistical modeling techniques to accomplish my objectives, which were as follows:

1. Evaluate the factors influencing American oystercatcher nest success across a mosaic of habitats

2. Identify the factors affecting American oystercatcher distribution in highly urbanized coastal ecosystems

3. Determine the extent of use of alternative breeding habitat (saltmarsh, inlet or back-bay islands) by American oystercatchers in New Jersey

4. Provide a more accurate estimate of the American oystercatcher breeding population in New Jersey

The first objective of my dissertation is examined in Chapter 1: The Effects of Predator-Free Islands in Sustaining American Oystercatchers within an Urbanized Barrier Island Complex. Here, I analyze the factors influencing American oystercatcher nest success in New Jersey. I focus on the differences in nest success rates between alternative habitat types, using a novel modeling approach to distinguish between the effects of habitat choice, predation pressure and human disturbance on daily nest survival rates.

The last three objectives of my research are examined in Chapter 2: Predicting American Oystercatcher Distribution in an Urbanized Coastal Ecosystem Using Maximum Entropy Modeling and Chapter 3: The Effect of Human Disturbance on the Local Distribution of American Oystercatchers Breeding on Barrier Island Beaches. In Chapter 2, I use a novel species distribution modeling technique to predict the realized niche of American oystercatchers across a mosaic of habitats along the entire New Jersey Atlantic coastline. A maximum entropy modeling technique was used to examine the influence of environmental variables and extent of coastal development on the distribution. The distribution model was then used to predict areas where oystercatchers may be breeding, and these predictions were tested with ground surveys in an effort to locate new oystercatcher populations in previously unsurveyed areas.

In Chapter 3, I use the results of the model developed in Chapter 2 as the starting point to conduct further exploration into the effect of human disturbance on the local distribution of American oystercatchers on New Jersey barrier beaches. I used several species distribution modeling techniques including classification and regression trees, random forests and maximum entropy modeling to examine how recreational disturbance on barrier beaches further influences the local distribution.

The main chapters of my dissertation were written as a series of stand-alone manuscripts that were formatted specifically for target journals. As such, each chapter is formatted differently. Additionally, the manuscripts were written in the first-person plural to indicate that they were written with my dissertation advisor, Julie L. Lockwood, as co-

author. The target journals are as follows: Chapter 1 – Conservation Biology, Chapter 2 – Diversity and Distributions, and Chapter 3 – Animal Conservation.

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CHAPTER 1

Predator-Free Islands Help Sustain American Oystercatchers within an Urbanized Barrier Island Complex

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Abstract: Urbanization on the barrier islands along the Atlantic coast of North America has severely altered the traditional breeding habitat for many beach-nesting birds in this region, including the American oystercatcher. We used an information theoretic approach to analyze various human-induced effects on oystercatcher daily nest survival rates and overall reproductive performance in an urbanizing coastal ecosystem. We used explanatory variables including habitat type, level of human disturbance, presence of mammalian predators, gull density and nest position as nest-specific covariates in our models to explore their effects on the daily survival rates of clutches and broods separately. We found an overall nest success rate of 4% in our study areas, which is far below the level necessary to sustain the local population. The principal factor negatively influencing daily survival rates of both clutches and broods was the presence of mammalian predators. Correspondingly, the nest success rate on predator-free islands (21%) was an order of magnitude greater than the rate reported on barrier islands (2%),

which have relatively high densities of predatory mammals. These findings show that protecting and managing alternative breeding habitats may be the best way to ensure the long-term population viability of American oystercatchers. This protection strategy may also have spillover benefits for other beach-nesting birds and wading birds.

Keywords: American oystercatcher, nest success, predator-free islands, program MARK

Introduction

Beach-nesting birds are in sharp decline worldwide in large part because of increasing loss or alteration of critical breeding habitat, human disturbance of breeding grounds, and mammalian predation pressure (Erwin et al. 2001; Gochfeld 1977; Lowney et al. 2005; Patterson et al. 1991). The beginning of these declines came between 1930-1970, coinciding with the first period of intensive coastal development in North America (Nisbet & Spendelow 1999). Coastal development pressure continues to increase, so much so that coastal counties currently make up 17% of the total land area in North America but account for 53% of the total human population (Crossett et al. 2004). Given such intense development pressure on coastal ecosystems, with all the attendant ecological issues, a legitimate question is whether we can we expect beach-nesting birds to persist without sustained intensive management efforts. American oystercatchers (*Haematopus palliatus palliatus*) are a prime example of a species facing this dilemma. They are a species of high conservation concern throughout their North American range because of their low population numbers and recently observed rapid range-wide population declines (Davis et al. 2001; Nol et al. 2000). Here we evaluate the breeding success of oystercatchers within a highly urbanized coastal barrier island ecosystem. We show an order of magnitude difference in breeding success across habitat types, with particularly high success on predator-free inlet and back-bay islands. Our results suggest that preserving these natural refuges can add substantially to the viability of oystercatcher populations, as well as other shorebirds, while avoiding costly management actions.

Prior to World War II, the coastline of the United States remained in a relatively natural state with more than 90% of barrier island complexes undeveloped and largely

inaccessible to the public. This situation changed dramatically over the next several decades and perhaps nowhere more pronounced than in the Mid-Atlantic region. In the state of New Jersey, total urbanized coastal barrier acreage reached 37% by 1950 and 47% by the mid-1970s (USFWS 1996). Coastal development in New Jersey has slowed in some areas in recent years, but the condition of coastal habitats has already been altered so severely in many instances that the species utilizing these habitats for breeding have experienced severely reduced reproductive success. Since the population consequences of reproductive failure are postponed in long-lived species with delayed maturity (Hernandez-Matias et al. 2003), a trait shared by many of the beach-nesting species in the order Charadriiformes, North American beach-nesting birds such as the American oystercatcher warrant high conservation concern.

Over the last several decades the American oystercatcher has expanded its range north along the Atlantic coast of the United States (Davis et al. 2001; Nol 1994; Post & Raynor 1964), and it was during this time that the species began to utilize non-traditional habitat to breed (e.g. saltmarsh), possibly facilitating the range expansion (Humphrey 1990; Post & Raynor 1964). In Chapter 2, we establish that the New Jersey oystercatcher population utilizes a mosaic of habitats for breeding including barrier beach strands, saltmarsh, natural inlet islands and artificial dredge-spoil islands, many of which are highly disturbed (especially as compared to breeding areas for more southerly populations). The use of alternative breeding habitats from the traditional barrier beach strand habitat historically used by American oystercatchers is becoming more widespread throughout the species' range (Lauro & Burger 1989; McGowan et al. 2005; Shields &

Parnell 1990; Wilke et al. 2007). However, at present there has been little comprehensive study of the effect this habitat shift may be having on population dynamics.

Lauro and Burger (1989) examined the nest site selection of oystercatchers breeding in saltmarsh habitat in New Jersey; however, these authors did not examine the differences in nest success between various habitat types. More recently, McGowan et al. (2005) examined the difference in nest success between barrier beach and river island habitats in North Carolina and found that hatching success was significantly greater on river islands; however, fledging success was lower resulting in no significant difference in overall nest success. Gaining a better understanding of the effects of the recent habitat shift on oystercatcher productivity is paramount in developing conservation strategies for the species.

Methods

Study Areas

We collected reproductive data at three study areas located in southern New Jersey with relatively high densities of breeding oystercatchers (Fig. 1). The availability of potential oystercatcher breeding habitat was similar at each site. Potential breeding habitat included barrier beach strands, adjacent saltmarsh systems and nearby inlet or dredge-spoil islands. All of the study areas were located on the north side of inlets that were breaks in the barrier island system. Controlling for the availability of alternate breeding habitat for oystercatchers at each study area provided us with replicates for each habitat type.

The three study areas represented a gradient of human disturbance from low- to high-use areas allowing analysis of the effects of human disturbance on oystercatcher reproductive rates. The Island Beach (IB) study area was the most heavily disturbed site in our study (Fig. 1). The New Jersey Division of Parks and Forestry manages Island Beach, which is the second highest use state park in New Jersey. The Holgate (HG) study area was the least disturbed site in our study (Fig. 1). The United States Fish and Wildlife Service manages Holgate as part of the Edwin B. Forsythe National Wildlife Refuge. Access was restricted during most of the breeding season primarily due to the presence of federally endangered breeding piping plovers (*Charadrius melodus*). Finally, the Stone Harbor (SH) study site experienced a moderate level of human disturbance (Fig. 1). The New Jersey Division of Fish and Wildlife – Endangered and Nongame Species Program (ENSP) manages the beach strand and inlet island habitat at SH, which is important breeding habitat for a number of threatened and endangered beach-nesting birds (e.g. piping plover, black skimmer *Rinchops niger*, least tern *Sternula antillarum*). As part of the management plan for this site, ENSP restricted access to large parts of the breeding areas used by beach-nesting birds including American oystercatchers.

Nest Searches and Monitoring

We searched for oystercatcher nests from 1 April to 31 July during each year of our study (2005-2006). We conducted nest searches by walking line transects following barrier beaches and the perimeters of inlet and dredge-spoil islands. We searched for nests in saltmarsh habitat by boat, following all navigatable shorelines and tidal creeks. We also conducted nest searches by walking line transects spaced 100 m apart in all interior

saltmarsh areas that were not accessible by boat. We located nests by intensifying searches in areas where we observed breeding behavior by adult oystercatchers. Typically, nests were located during the egg-stage (n = 205); however, we did locate nests during the nestling-stage as well (n = 6). Most nests located during the egg-stage were found prior to clutch completion (n = 147, mean number of eggs when found = 1.9, SD = 0.8).

We monitored nests every 3-7 days (mode = 3.0, mean = 5.1, SD = 3.3) until the nest either successfully fledged at least one young or all nest contents were lost to predation or flooding. Clutch failure was determined when nestlings were not observed, or if there were an absence of behavioral cues that would indicate hatching (described below) after the expected hatch date and/or when the entire clutch had disappeared. A clutch was considered to have hatched upon the observation of at least one nestling in or near the nest. We considered a brood as successful when at least one chick fledged, and we considered a nest to have failed when the entire brood was lost. We considered a brood lost when no nestlings were observed or when we observed no behavioral cues over two consecutive nest visits. In these instances we determined the date of failure as the first date that nestlings or behavioral cues were not observed. We determined the cause of failure for clutches based on evidence observed at the nest site, such as signs of flooding or predation, the latter including presence of broken eggshells in nests or animal tracks leading to failed nests. Causes of failure for broods were difficult to identify since nestlings often disappeared from territories without evidence.

We used a modeling approach that required accurate determination of transitions between nest stages (see below), thus we intensified nest searches near expected hatch

dates. We determined transition between these stages by observation of at least one nestling in the nest or by observation of certain behavioral cues by adults indicating that a clutch had hatched. The use of behavioral cues as an indication of hatching was necessary in order to obtain the most accurate estimate of transition date since nestlings could not be located during every nest visit. The behavioral cues included an increased vigilance by adults at nest sites, with adults exhibiting much more aggressive behavior in defense of territories upon approach. The aggressive behavior included a circling flight around observers while calling loudly with a unique, rapid, four-note staccato call that is used by adults predominantly when there is an active brood. We observed a few occasions where this behavior was used when clutches were near their expected hatch dates; however, in most instances this behavior was only observed after nests had hatched. In all cases where we relied on these behavioral cues to indicate transition between the egg- and nestling-stages we later confirmed hatching on subsequent nest visits by the observation of at least one nestling.

Factors Influencing Nest Success

We measured nest success as the daily survival rate (DSR) following Mayfield (1975). Recent incarnations of Mayfield's estimator allow investigators to evaluate the influence of factors on DSR using information-theoretic algorithms (see below). We included the following explanatory variables (covariates) in our nest survival models:

1. Nest Stage. Daily nest survival rates for precocial birds vary significantly between the incubation and nestling periods. We thus expected daily nest survival rates in our study to vary substantially across nest stages. We assigned

nests into two groups (egg-stage or nestling-stage) to assess differences between stages, with some nests included in both groups if they persisted past the egg-stage.

2. Year. Oystercatchers are known to exhibit high annual variability in nest success (Davis et al. 2001; Nol 1989). Therefore, we included year as a covariate in our models to assess annual differences in oystercatcher nest survival.

3. Habitat. We assigned all nests into one of three habitat categories: beach, marsh or island. Beach nests were those located on major barrier island beach strands. Beach nests were typically placed in open areas with sandy substrate and little vegetation. Marsh nests were those located in *Spartina* dominated saltmarsh including areas of marsh attached to barrier islands and in some cases small, isolated saltmarsh islands. American oystercatchers typically placed nests in wrack deposits (dead vegetation) within marsh habitat. Island nests were those located on natural inlet islands or artificial dredge-spoil islands. These nests were usually placed in open areas with sandy substrate similar to beach nests; however, they were also placed in dense vegetation (e.g. *Phragmites australis*) or on wrack deposits on dredge-spoil islands.

4. Gull Density Index. Gulls (*Larus spp.*) are known to be nest predators for a variety of beach-nesting species, and gull predation is a major cause of nestling mortality for oystercatchers (Hockey 1996). Abundant gull species found at our study sites during summer months included great black-backed gulls (*L. marinus*), herring gulls (*L. argentatus*) and laughing gulls (*L. atricilla*), all of which breed in close proximity to oystercatchers. During our nest monitoring visits, we

conducted visual circular point counts of all gull species within a 100 m radius of the oystercatcher nest. We recorded the seasonal mean of all point count estimates at each nest and used this mean as an index of gull density for that nest in our models.

5. Mammal Index. Mammalian predation is the leading cause of nest failure for many ground-nesting avian species, including American oystercatchers (Davis et al. 2001; McGowan et al. 2005; Sabine et al. 2006). Mammalian species regularly observed at our study sites included red fox (*Vulpes vulpes*), striped skunk (*Mephitis mephitis*) and raccoon (*Procyon lotor*). In order to assess the effect that mammals have on oystercatcher nest survival, we conducted surveys for mammal tracks or other signs within a 100 m radius of all oystercatcher nests during each periodic nest visit. During each nest visit, a binary code was recorded indicating the presence (1) or absence (0) of mammal tracks or signs on each oystercatcher territory. We used these data to calculate the proportion of visits over the course of the monitoring period that we recorded mammal activity at each territory.

6. Disturbance Index. The effects of human disturbance on oystercatcher nest survival is unknown; however, McGowan et al. (2006) provided evidence that human disturbance can alter oystercatcher incubation behavior. It is probable that high rates of human activity on breeding grounds can disrupt oystercatcher incubation behavior leading to lower nest survival rates through inducing inappropriate incubation temperatures or increased nest predation due to exposure of nests during forced departures. In order to assess the effect of human

disturbance on oystercatcher nest survival, we assigned an index for human activity to each nest. During each nest visit, a binary code was recorded indicating the presence (1) or absence (0) of human activity within a 100 m radius surrounding each oystercatcher nest. We used these data to calculate the proportion of visits over the course of the monitoring period that we recorded human activity on or near each territory.

7. Nest Position. The position of oystercatcher nests near the tide line makes them particularly susceptible to flooding (Lauro & Burger 1989; Nol 1989). Therefore, we expected that the position of the nest above mean sea level would influence nest survival. We assigned each nest one of three rankings: (1) low, (2) medium and (3) high. Low nests were those located in areas that we considered susceptible to flooding caused by monthly spring tides. Medium-height nests were those nests located in areas that we expected to be safe from flooding caused by monthly spring tides, but susceptible to flooding from storm tides. High nests were those nests located in areas that we expected to be safe from flooding from all but the most severe storm tides.

Data Analysis

We estimated daily survival rates of oystercatcher nests using the nest survival model (Dinsmore et al. 2002) in program MARK (White & Burnham 1999). This software uses generalized linear models within a maximum likelihood approach to estimate DSR (Rotella et al. 2004). We used a hierarchical approach to generate a candidate set of *a priori* models for use in our analyses, similar to other recent studies using program

MARK (Colwell et al. 2007; Hood & Dinsmore 2007). We began our analyses by examining the effect of nest stage on DSR by coding our data into two groups and running models comparing constant and time-varying DSR with and without a group (stage) effect, excluding any additional nest-specific covariates.

As expected, we found large differences in DSR between the two stages (egg and nestling, see below). Thus, we generated a set of *a priori* models examining the effects of various explanatory variables (covariates) on oystercatcher DSR during the egg- and nestling-stages separately. All generalized linear models that incorporated one or more covariates used the logit link function and all other models used the sin link function (Burnham & Anderson 2002). We ranked competing models that describe the relationship between DSR and explanatory variables using Akaike's Information Criterion (AIC_c) corrected for small sample size (Burnham & Anderson 2002). We judged models with ΔAIC_c values < 2.00 as having substantial support, ΔAIC_c values from 2.00 − 7.00 having considerably less support, and ΔAIC_c values > 7.00 indicating essentially no support (Burnham & Anderson 2002). The effect of each explanatory variable on nest survival is represented by the beta (β) estimate for each covariate provided by program MARK. Strong effects were inferred by beta estimates with good achieved confidence interval coverage that did not cross zero (Burnham & Anderson 2002).

Due to high predation rates at our study areas, it was difficult to accurately determine whether nests were in the egg-laying or incubation stages. As such, for purposes of our nest survival modeling, we combined all nests with eggs, regardless of timing within the egg-stage, into our clutch survival models. Additionally, since

individual nestlings were difficult to observe during each nest visit, we decided to model brood survival rather than individual nestling survival. We were able to accurately determine the fate of broods based on direct observation of nestlings or behavioral cues, as described previously. In such cases, it is more appropriate to model brood survival than individual nestling survival rates (Colwell et al. 2007).

Within our stage-specific models, we generated separate sets of *a priori* candidate models that described competing hypotheses (Table 1). We developed a set of 19 *a priori* models explaining DSR of clutches and 19 *a priori* models explaining brood survival. We used a similar set of models at each stage in order to understand the factors that influence DSR during each stage of the nesting cycle for American oystercatchers since these factors may or may not be similar.

We hypothesized that oystercatcher nest survival would vary between habitat type and year, and that clutch survival would be affected by nest position (see above, Nol 1989). We also hypothesized that predator activity would lead to reduced survival rates at both nest stages; however, we expected there to be different effects at each stage depending on type of predator. We included models that incorporated an interaction between predator activity and human disturbance since it is possible that human activity on breeding grounds could influence predation rates positively or negatively. In our brood survival models, we included an interaction term between our habitat and predator covariates since there may be differential nestling predation rates in habitats with different vegetation characteristics.

In order to illustrate the effects of various covariates on overall oystercatcher nest success, we used the DSR of clutches and broods to extrapolate hatching and fledging

success rates, respectively (Johnson 1979). We raised the DSR estimate based on the best approximating model for each stage to a power indicating the total number of exposure days of each stage (hatching = 28 days; fledging = 42 days). Overall nest success was calculated by multiplying hatching and fledging success rates (Johnson 1979). Standard errors for hatching and fledging success rates were calculated by multiplying the standard error reported by program MARK for each stage-specific DSR estimate by the derivative of the DSR estimate (Powell 2007). The standard error for nest success was calculated using the delta method (Powell 2007; Seber 1982).

Results

Nest Success

We monitored 205 American oystercatcher nests with eggs and 61 broods during the 2005 and 2006 breeding seasons, with reasonably large numbers of nests distributed across all habitats. Based on the best models for clutch and brood survival, the overall nest success rate for New Jersey oystercatchers was extremely low at 0.038 (SE = 0.002). Contrary to expectations that the optimal breeding habitat for American oystercatchers should be barrier beach habitat, oystercatchers in New Jersey experienced their lowest reproductive rates in this habitat. Hatching success was lowest on barrier beaches at 0.058 (SE = 0.001) and highest on isolated islands at 0.37 (SE = 0.03) where there was an almost complete absence of mammalian predators (Fig. 4). The hatching success rate for marsh breeding oystercatchers was 0.20 (SE = 0.01), which is a habitat where nests are also exposed to mammalian predators. Fledging success was also lowest on barrier beaches at 0.33 (SE = 0.04) and highest on isolated islands at 0.55 (SE = 0.05); however,

marsh breeders experienced a similar fledging success rate as nests on isolated islands at 0.52 (SE = 0.08). The differential hatching and fledging success rates across habitat types resulted in substantially higher overall productivity (nest success) for island breeding oystercatchers in New Jersey. In fact, nest success for island nesting oystercatchers was 0.21 (SE = 0.03), which is almost twice that of marsh nesting pairs (0.11, SE = 0.01) and an order of magnitude greater than barrier beach nesting pairs (0.019, SE = 0.001).

Stage Models

In our initial MARK analysis of the effect of nest stage and time on DSR, we found that the model that included only nest stage received all of the support in this analysis (Table 2; normalized Akaike weight (w_i) of 1.0). The strong difference in DSR between stages was further highlighted by the very high ΔAIC_c between the best-supported model and the next model (i.e. the constant survival model that excludes stage) of 47.79. Time-varying survival models received no support in this initial analysis.

American oystercatcher clutches had substantially lower DSR than broods ($DSR_{clutches}$ = 0.94, SE = 0.01; DSR_{broods} = 0.983, SE = 0.003). These results confirm our expectation that breaking our dataset into two discrete groups for all further analyses was warranted as this allowed us to examine the effects of nest-specific covariates on survival during each stage separately. Additionally, all further analyses assumed constant nest survival rates since time-varying models received no support in our initial analysis.

Clutch Survival

Our clutch survival models indicated that an additive model including covariates for gull density, mammal activity and nest position was the best supported (w_i = 0.80; ΔAIC_c difference of 3.00). This model received substantially all of the support in our analysis (Table 3). The DSR of oystercatcher clutches based on the best-supported model was 0.93 (SE = 0.01). The negative effect of mammals on clutch survival was substantial (β = -2.51, 95% CI = -3.28, -1.75), whereas nest position had a positive effect on clutch survival (β = 0.56, 95% CI = 0.28, 0.84). Gull density also had a positive effect on clutch survival; however, the effect size was very small (β = 0.007, 95% CI = 0.002, 0.012).

One of the benefits of using program MARK to model nest survival is that it provides a method to predict DSR based on the best-supported model (Dinsmore & Dinsmore 2007). For illustrative purposes, we examined the effect of different levels of mammal activity on the survival of oystercatcher nests that were susceptible to flooding (low position category) versus those that were not (high position category; Fig. 2). Our predictive analysis illustrates the large difference in DSR between nests likely to flood (low nests) versus those that were not (high nests), and more importantly, the substantial decline in DSR as the level of mammal activity increased within oystercatcher territories regardless of nest position (Fig. 2).

Brood Survival

The model that included an interaction between mammal activity and human disturbance received substantially all of the support in this analysis (w_i = 0.75, ΔAIC_c difference of 3.47, Table 4). The DSR of oystercatcher broods based on the best-supported model was 0.97 (SE = 0.02). As with our clutch survival models, our brood survival models

indicated a substantial negative effect of mammals on DSR during this stage (β = -14.92, 95% CI = -23.47, -6.37). The best model indicated that human disturbance also negatively effects brood survival; however, the confidence interval for this parameter crosses zero (β = -1.01, 95% CI = -4.63, 2.61). The interaction term between mammal activity and human disturbance indicated a substantial positive effect on brood survival; however, the confidence interval coverage for this parameter was very wide (β = 107.79, 95% CI = 1.42, 214.17). The poor confidence interval coverage of the human disturbance covariate and interaction terms indicates lower resolution in our brood survival models as compared to our clutch survival models.

To illustrate the effect of mammal presence and human disturbance on oystercatcher brood survival we predicted brood DSR in response to varying levels of these covariates (Fig. 3). Mammal activity negatively affects brood survival, but there was an indication that human activity moderated the ill effects of mammals leading to reduced predation on nestlings (Fig. 3).

Discussion

Breeding success for American oystercatchers in New Jersey was low, especially compared to more southerly breeding areas outside of New Jersey. Oystercatcher nests were much more likely to fail at the egg-stage rather than the nestling-stage. As such, the low nest success rates reported were driven primarily by the extremely low hatching success rates, which ranged from 6% on barrier beaches to 37% on isolated islands. These rates were well below hatching success rates recently reported further south along the Atlantic coast. For example McGowan et al. (2005) and Sabine et al. (2006) reported

hatching success rates as high as 45% in North Carolina and Georgia respectively. Most alarming was the extremely low nest success rate we found for oystercatchers breeding on New Jersey barrier beach strands (2%), which was substantially below the success rates reported on barrier islands in more southern parts of the oystercatcher's range (11–14%) (Davis et al. 2001; McGowan et al. 2005; Nol 1989). Based on population viability analyses for North Carolina oystercatchers, Brown et al. (2008) show that nest success must be above 18% just for the population to remain stable over the next 10 years. The reproductive rates we reported for New Jersey oystercatcher's breeding along barrier beach strands, which is the preferred habitat for the species, are thus very far below what might be considered sustainable.

We did observe a very large difference in nest success rates between habitats, and this may provide a potential avenue for conserving this species over the long-term. In particular, the survival rates we calculated translated into a 21% chance that a given oystercatcher egg laid will result in an independent juvenile on inlet or dredge-spoil islands. This rate was an order of magnitude higher than what we observed on barrier beach strands. The differential success rate between habitats was most pronounced during the egg-stage, where hatching success ranged from 6% on beach strands to 37% on isolated islands. The same pattern held for fledging success, where rates ranged from 33% on beach strands to 55% on isolated islands. The single factor that consistently showed a large effect on success, and best explained our observed differences between habitats, was mammalian predation. Indeed, the importance of islands as a refuge from mammalian predation was magnified as oystercatcher nests matured. The effect size for mammalian predation was seven times larger in the nestling-stage than the egg-stage.

This trend is true despite the fact that most nesting attempts in areas with high mammal density failed during the egg-stage prior to hatching, and thus nestling-stage models included few nests from high mammal density areas such as barrier beach strands.

The heavy influence of mammalian predators on American oystercatcher nest success is not surprising since mammalian predation has been linked to low reproductive success for oystercatcher species throughout the world (Davis et al. 2001; Gill et al. 2004; Hockey 1996). More generally, mammalian predators are associated with reduced reproductive rates, population declines and the extinction of many avian species on oceanic islands due to a lack of defenses in island birds that evolved without the threat of terrestrial predators (Atkinson 1996; Blackburn et al. 2004; Blackburn et al. 2005). Although perhaps not as isolated from continental influences as many oceanic islands, the barrier islands off the Atlantic coast of eastern North America formerly functioned as refuges from mainland populations of mammalian predators for many of the region's threatened and endangered shorebird species. Predator movements from the mainland to islands and between islands do occur (Dueser et al. 2005). However, historic population levels of mammalian predators on barrier islands were likely lower than current levels due to the harsh conditions on these coastal islands and because of barriers to immigration that existed before automobile bridges were built connecting many of the barrier islands to the mainland (Patterson et al. 1991).

In addition, important native mammalian nest predators have undergone recent range expansions as a result of coastal development and associated anthropogenic food subsidies (Burger & Lesser 1980). Food subsidies provided by human garbage are often associated with increased predator abundances due to the better physical condition of

individuals in the population, decreased mortality rates (especially winter mortality), increased reproductive rates, and higher annual recruitment into predator populations (Burger & Lesser 1980; Patterson et al. 1991). Human food subsidies may not only help sustain higher predator populations on barrier islands; subsidies on the extensively developed mainland may help ensure a constant source of migrants onto the barrier islands.

In response to the loss or deterioration of barrier island habitat due to coastal urbanization and heavy predation pressure, many beach-nesting species including the American oystercatcher have already begun to use alternative breeding habitat such as saltmarsh, riverine, inlet or back-bay islands. These small islands are often more isolated than barrier islands and thus often do not have persistent populations of mammalian predators. Our results suggest that the importance of these alternative islands for beach-nesting birds cannot be understated. Our results are consistent with other studies (McGowan et al. 2005) showing that American oystercatcher nest densities and success are higher on isolated islands than adjacent barrier islands. The creation of predator-free islands in coastal Virginia as a result of extensive predator removal efforts has led to increased productivity for piping plovers and American oystercatchers, and breeding population increases for a number of other threatened or endangered birds (Dueser et al. 2005). The complete removal of raccoons and red foxes on several islands resulted in significantly improved productivity for a suite of avian species. Similar results were found for oystercatchers breeding in North Carolina following red fox control (McGowan 2004).

If beach-nesting birds are already selecting smaller, isolated islands as replacements for large barrier islands for breeding, the protection of these islands becomes central to conservation management. Predators can be controlled more easily on smaller islands (Dueser et al. 2005; Parkes & Murphy 2003). In fact, complete removal of mammalian predators is possible on small islands whereas it may be impractical on large barrier islands. As such, the long-term monetary and labor costs of predator control efforts would be substantially lower than similar efforts on larger barrier islands. Additionally, it is likely that conservation managers would meet with less public opposition to predator removal programs on isolated islands that are separated from residential areas rather than targeting efforts on barrier beaches that are highly desirable recreational sites.

Given the importance of isolated islands for breeding shorebirds in eastern North America, a viable management option over the long-term is to secure more isolated natural islands or create more artificial dredge-spoil islands. Furthermore, existing islands could be managed to create optimal breeding habitat for a suite of beach-nesting species (e.g. remove vegetation or increase island height). The protection of many isolated islands of various types would benefit beach-nesting birds by allowing more colonies to become established thus reducing overcrowding at existing colonies, reducing competition with other species such as gulls, and spreading the risks associated with stochastic events over more sites. Additionally, having many isolated islands would make alternative sites available in the event that mammalian predators colonize an existing breeding site.

Acknowledgements

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Tables

Table 1: Hypothesized effects of model covariates and interactions on daily survival rates of oystercatcher clutches and broods in coastal New Jersey (2005 – 2006).

Covariate/Interaction	Clutch Survival	Brood Survival
Year	High variation in survival rate between years	Same hypothesis
Habitat type	Higher survival rate on barrier beaches than in alternate habitats	Same hypothesis
Avian predators (gulls)	High level reduces survival rate to lesser degree	High level reduces survival rate substantially
Mammalian predators	Mammal presence reduces survival rate substantially	Mammal presence reduces survival rate to lesser degree
Human disturbance	High level reduces survival rate substantially	Same hypothesis
Nest position	Lower nests have reduced survival rates	Not included in model set
Interaction between predator levels and human disturbance	May increase survival rate	Same hypothesis
Interaction between predator levels and habitat type	Not included in model set	Reduced survival rate in marsh habitat
Interaction between year and habitat type	Interaction due to variation in annual flooding	Same hypothesis

Table 2: Model selection results for nest-stage models assuming constant and time-varying daily survival probabilities for American oystercatchers in coastal New Jersey (2005 – 2006).

Model[a]	AIC_c[b]	ΔAIC_c	w_i[c]	K[d]	Deviance
DSR$_{constant}$ + Stage	773.63	0.00	1.00	2	769.63
DSR$_{constant}$	821.43	47.79	0.00	1	819.42
DSR$_{time}$	921.96	148.32	0.00	104	707.45
DSR$_{time}$ + Stage	1051.73	278.09	0.00	183	665.16

[a]Models ranked by ΔAIC_c in ascending order. Additive models indicated by +.

[b]Akaike's information criteria adjusted for small sample size.

[c]AIC model weight.

[d]Number of parameters.

Table 3: Model selection results for clutch survival models for American oystercatchers in coastal New Jersey (2005 – 2006).

Model[a]	AIC$_c$[b]	ΔAIC$_c$	w_i[c]	K[d]	Deviance
Gull + Mammal + Nest Position	519.87	0.00	0.80	4	511.85
Year + Habitat + Gull + Mammal + Disturb + Nest Position	522.88	3.00	0.18	8	506.81
Mammal + Nest Position	527.41	7.53	0.02	3	521.40
Year*Habitat	531.38	11.50	0.00	6	519.34
Gull + Mammal	534.06	14.19	0.00	3	528.05
Gull*Disturb + Mammal*Disturb	534.09	14.22	0.00	6	522.05
Gull + Mammal + Disturb	536.00	16.13	0.00	4	527.98
Mammal*Disturb	547.92	28.04	0.00	4	539.90
Mammal	548.29	28.41	0.00	2	544.28
Mammal + Disturb	549.14	29.27	0.00	3	543.13
Year + Habitat	556.88	37.00	0.00	4	548.86
Habitat	557.00	37.13	0.00	3	550.99
Gull	557.40	37.52	0.00	2	553.39
Gull + Disturb	557.95	38.07	0.00	3	551.93
Gull + Nest Position	558.27	38.40	0.00	3	552.26
Gull*Disturb	559.49	39.62	0.00	4	551.47
Nest Position	581.36	61.48	0.00	2	577.35
DSR$_{constant}$	582.60	62.73	0.00	1	580.60

Year	583.12	63.24	0.00	2	579.11
Disturb	584.31	64.43	0.00	2	580.30

[a]Models ranked by ΔAIC_c in ascending order. Additive models indicated by +, models with interaction terms indicated by *.

[b]Akaike's information criteria adjusted for small sample size.

[c]AIC model weight.

[d]Number of parameters.

Table 4: Model selection results for brood survival models for American oystercatchers in coastal New Jersey (2005 – 2006).

Model[a]	AIC_c[b]	ΔAIC_c	w_i[c]	K[d]	Deviance
Mammal*Disturb	182.70	0.00	0.75	4	174.67
Gull*Disturb + Mammal*Disturb	186.16	3.47	0.13	6	174.11
Habitat*Gull	188.91	6.22	0.03	6	176.86
Year*Habitat	189.70	7.00	0.02	6	177.64
Year	190.82	8.12	0.01	2	186.81
$DSR_{constant}$	191.03	8.33	0.01	1	189.03
Mammal	192.72	10.02	0.01	2	188.71
Disturb	192.84	10.14	0.00	2	188.83
Gull	192.94	10.25	0.00	2	188.94
Habitat	193.26	10.57	0.00	3	187.25
Habitat + Gull	193.83	11.13	0.00	4	185.80
Year + Habitat	194.39	11.69	0.00	4	186.36
Habitat + Mammal	194.57	11.87	0.00	4	186.54
Mammal + Disturb	194.61	11.91	0.00	3	188.59
Gull + Mammal	194.67	11.97	0.00	3	188.65
Gull + Disturb	194.84	12.14	0.00	3	188.82
Gull + Mammal + Disturb	196.61	13.91	0.00	4	188.59
Gull*Disturb	196.68	13.98	0.00	4	188.65
Habitat*Mammal	197.87	15.17	0.00	6	185.81

| Year + Habitat + Gull + Mammal + Disturb | 198.46 | 15.76 | 0.00 | 7 | 184.38 |

[a]Models ranked by ΔAIC$_c$ in ascending order. Additive models indicated by +, models with interaction terms indicated by *.

[b]Akaike's information criteria adjusted for small sample size.

[c]AIC model weight.

[d]Number of parameters.

Figure Legends

Figure 1: Location of three breeding areas included in our 2005 – 2006 study of breeding American oystercatchers: (1) the Southern Natural Area of Island Beach State Park (IB) located in Ocean County, New Jersey (39.77 N, -74.10 W), (2) the Holgate Division of the Edwin B. Forsythe National Wildlife Refuge (HG) also located in Ocean County (39.50 N, -71.30 W), and (3) Stone Harbor Point (SH) located in Cape May County (39.03 N, -74.78 W). The habitat available for breeding oystercatchers at Island Beach (IB) includes 3.3 km of undeveloped barrier beach, a 1.6 km artificial inlet beach along a dike created by the Army Corp of Engineers, approximately 197 hectares of adjacent saltmarsh located within the Sedge Island Marine Conservation Zone, and an 8 hectare artificial dredge-spoil island located within Barnegat Inlet referred to as Gull Island. The habitat available for oystercatchers at Holgate (HG) includes 6.0 km of undeveloped barrier beach, approximately 74 hectares of saltmarsh located directly adjacent to the barrier beach strand, and a 5 hectare naturally-forming inlet island located within Little Egg Inlet known as Tuckers Island. The habitat available for oystercatchers at Stone Harbor (SH) includes 1.8 km of partially developed barrier beach, approximately 23 hectares of saltmarsh located directly adjacent to the barrier beach strand, a 126 hectare nearby saltmarsh island known as Nummy Island, and an 11 hectare naturally-forming inlet island located within Hereford Inlet known as Champagne Island.

Figure 2: Predicted daily survival rate of American oystercatcher clutches in response to mammal activity and nest position in coastal New Jersey (2005 – 2006). Daily survival

rate was based on the best clutch survival model (Mammal + Gull + Nest Position) setting nest position to either high or low and allowing the mammal index to range from 0.0 to 1.0, which were levels reported for actual nests in our study. We set the gull density index at zero since the effect size for this covariate on DSR was negligible.

Figure 3: Predicted daily survival rate of American oystercatcher broods in response to mammal activity and human disturbance in coastal New Jersey (2005 – 2006). Daily survival rate was based on the best brood survival model (Mammal*Disturb), which included an interaction term between the covariates. In this analysis we allowed the mammal index to range from 0.0 to 1.0 and set the disturbance index (DI) to three levels (0.00, 0.10, 0.20), all of which were towards the lower end of the range reported in our study.

Figure 4: American oystercatcher reproductive rates by habitat type in coastal New Jersey (2005 – 2006). Error bars represent SE calculated using the delta method. Numbers above the error bars represent sample sizes of clutches and broods included in the nest survival models used to calculate reproductive success rates.

Figures

Figure 1
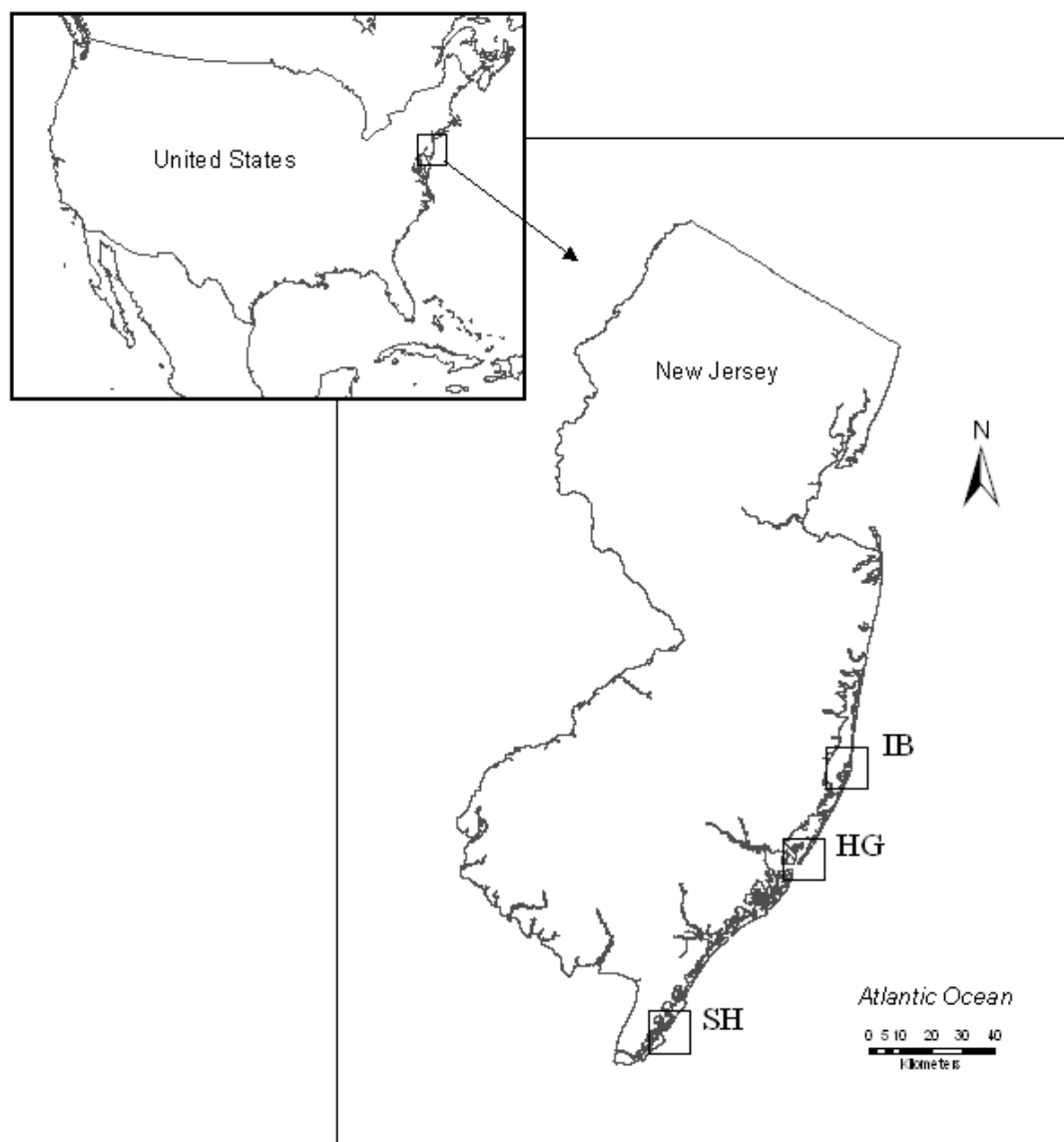
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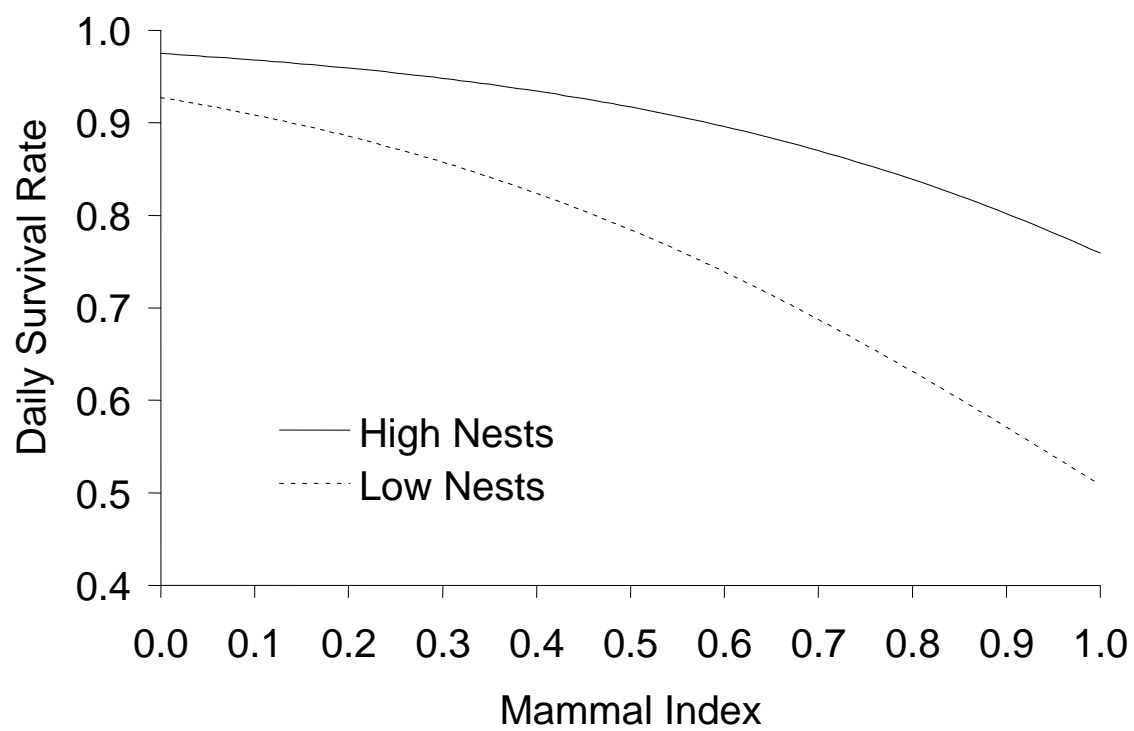
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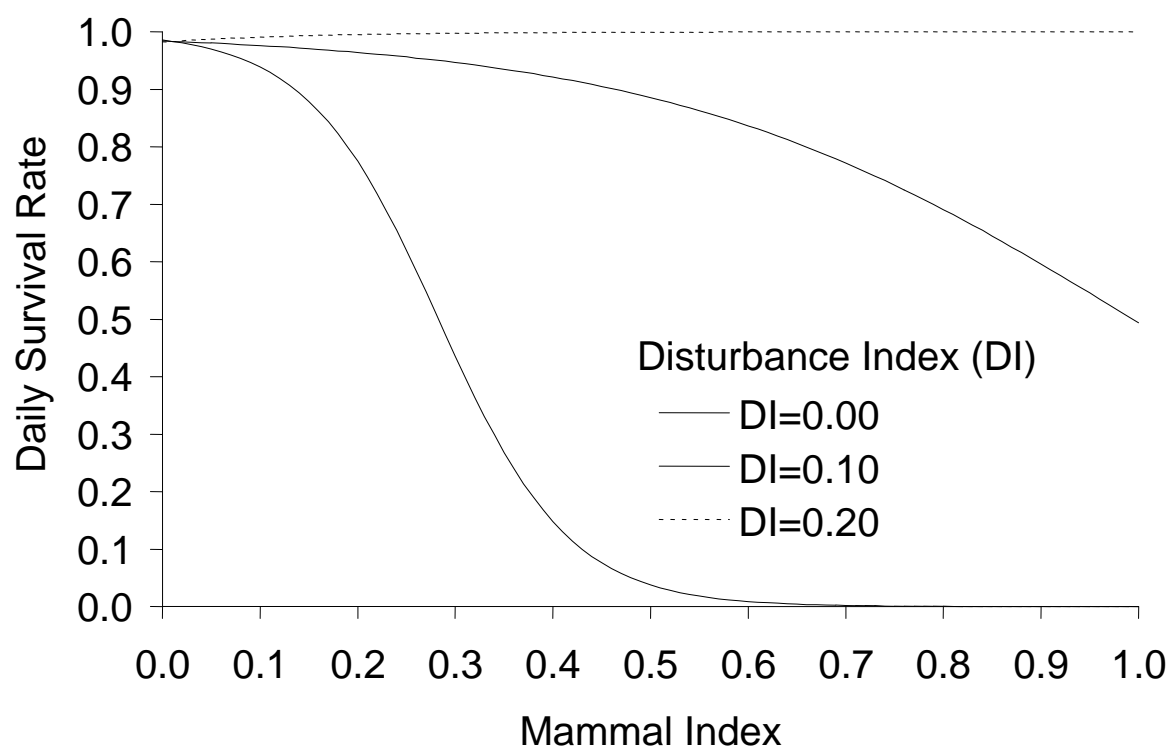
Figure 4
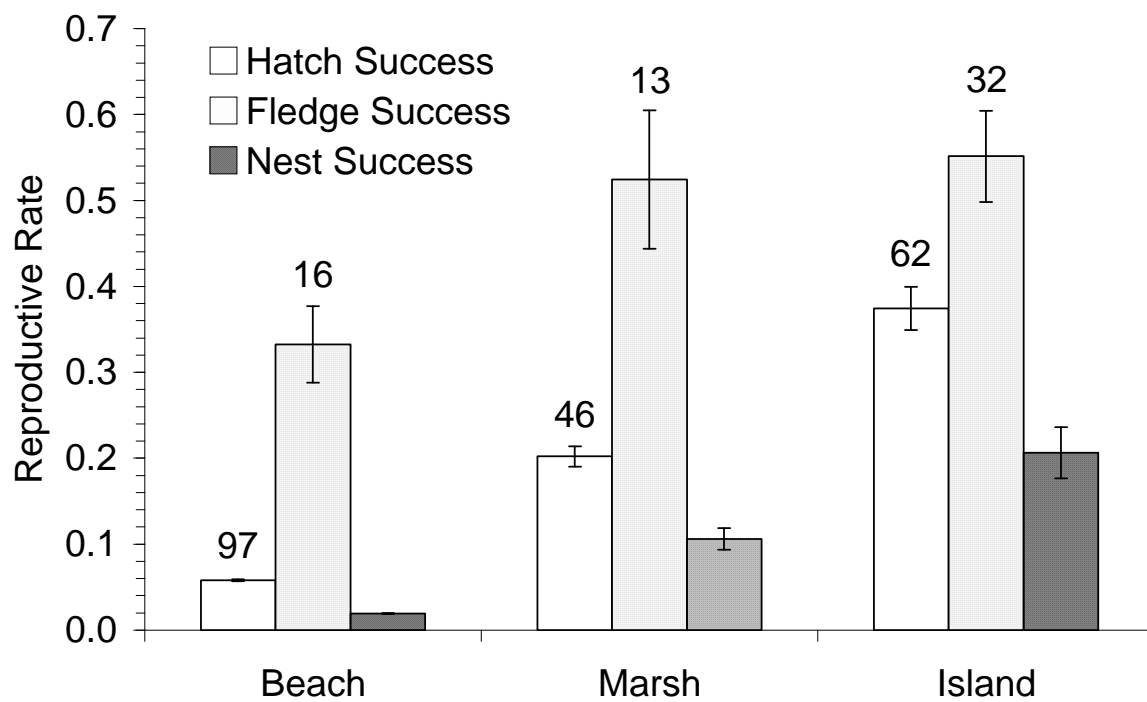
CHAPTER 2

Predicting American Oystercatcher Distribution in an Urbanized Coastal Ecosystem Using Maximum Entropy Modeling

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ABSTRACT

Species distribution modeling has seen widespread use in ecology and conservation over the past two decades, and as a result many questions regarding the predictive capabilities of new techniques have been raised. One modeling approach that has gained popularity is the MAXENT software, which uses presence-only data to model species' distributions. Although MAXENT is ordinarily used to model a species fundamental niche at large scales (e.g. continental-scale), we have used this technique to model the realized niche and local distribution of the American oystercatcher (*Haematopus palliatus palliatus*) at a

fine-scale. We examined the transferability of our predictive model to areas outside the training areas in an effort to locate new populations in previously unsurveyed areas. We then evaluated model performance with an independent validation dataset, which is rare in species distribution modeling. Our results showed that the MAXENT model provided predictions that were useful to locate new populations. Ground surveys based on our model located 185 previously unknown breeding pairs of oystercatchers in coastal New Jersey, which more than doubled the estimate of the local breeding population. However, validation of the MAXENT model with independent data provided by our ground surveys proved difficult. We attributed this to source-sink dynamics that affected the actual distribution of oystercatchers at a local scale rather than to errors in our modeling technique. We suggest that future researchers attempting to validate species distribution models with ground surveys take into consideration metapopulation and source-sink theory in the design of surveys and interpretation of results.

(A) INTRODUCTION

Species distribution modeling has been used to project species' responses to land use and climate change, predict invasive species geographic limits, identify new species or populations, and establish biodiversity reserve networks (Araujo et al. 2005; Ficetola et al. 2007; Pawar et al. 2007; Raxworthy et al. 2003; Rodriguez-Estrella 2007). The increased use of species distribution modeling in ecology and conservation in recent years has led to a large body of literature comparing various techniques and exploring issues such as model application, selection, calibration, validation and transferability (Araujo & Guisan 2006; Elith et al. 2006; Guisan & Zimmerman 2000; Hirzel et al. 2006; Peterson 2006). We examined some of these issues using a novel presence-only modeling technique (MAXENT) to predict the distribution of American oystercatchers (*Haematopus palliatus palliatus*) in coastal New Jersey. We used a small dataset of known occurrence records collected at a local scale to model the species' distribution over a larger scale in an effort to predict the occurrence of oystercatchers in previously unsurveyed areas, and to evaluate our model's performance with an independent dataset.

Underlying the major issues concerning distribution modeling are the transferability of models and model validation (or evaluation) (Boitani et al. 2008; Loiselle et al. 2008; Peterson 2007; Phillips 2008). Transferability relates to the ability of a model to predict a species' distribution using information assembled from somewhere outside the focal area. Model validation is the process of measuring the accuracy between model predictions and actual observations, which can be done by a variety of methods (see Guisan & Zimmerman 2000). In order to evaluate the performance and transferability of a species

distribution model it is important to first understand what is being modeled so that comparison between model results and validation data can be better interpreted. The goal of many species distribution modeling techniques is to model a species' ecological niche, which is then used to predict its potential distribution over geographic space (Soberon & Peterson 2005). Many of the recent presence-only modeling techniques were designed to model a species' fundamental niche, defined as the set of abiotic environmental conditions necessary for a species' long-term survival (Hutchinson 1957). However, it is often difficult to distinguish in practice between a species' fundamental niche and its realized niche, which is a subset of the fundamental niche taking into consideration biotic interactions. Distinguishing between the fundamental and realized niche is especially difficult in highly modified landscapes where a species may never be expected to completely fill its fundamental niche (Peterson 2006; Pulliam 2000; Soberon & Peterson 2005).

Clarification of the niche concept is considered one of the major challenges in species distribution modeling (Araujo & Guisan 2006), and is an especially important consideration in any *a posteriori* attempt to evaluate the effectiveness of a species distribution model. Errors between predicted and actual occurrences should be expected since the training data (i.e. occurrence records used to develop the models) may better reflect the species' realized niche. In addition, the actual occurrence information might be further limited within the modeled realized niche if source-sink dynamics are affecting the species' local distribution (Pulliam 2000).

The scale at which the predictions are developed plays an important role in deciding whether a species' fundamental or realized niche is being predicted (Fielding & Bell 1997). Models developed at the regional or continental scale using broad-scale predictor variables such as temperature, precipitation or elevation may better predict the fundamental niche of the species. Models using fine-scale predictor variables such as nesting substrate type may better predict the realized niche (Karl et al. 2000). Certainly, at a more local scale, factors such as inter-specific competition or human disturbance play an important role in affecting a species distribution (Thuiller et al. 2004). Thus, consideration of scale must be weighed when evaluating model results with independent validation data derived from ground surveys.

The distribution of American oystercatchers in New Jersey provides a novel test of distribution models because this geographic area represents a recently re-colonized part of the species' range. After being extirpated from northern parts of the species' range by the early 1900s due to habitat loss and commercial hunting, oystercatchers have recently expanded north along the Atlantic coast of the United States (Nol & Humphrey 1994; Davis 2001). It was during this time that the species' local breeding distribution began to change, possibly facilitating the range expansion (Humphrey 1990). Such plasticity in oystercatcher breeding ecology is not unprecedented. The European oystercatcher (*H. ostralegus*) recently moved inland in several European countries shifting its breeding habitat from coastal areas to agricultural fields (Goss-Custard et al. 1997).

Understanding the current distribution of American oystercatchers is the first step towards planning conservation actions needed for this species of special concern. American oystercatchers face significant threats throughout their range including habitat loss, habitat degradation, human disturbance, potential prey resource depletion and increasing threats from predators (Brown et al. 2005). New Jersey is the most densely populated state in the United States, and ecosystems in the state's coastal zone are highly altered. At present, we do not have a clear understanding of oystercatcher distribution in urbanized coastal ecosystems, nor do we have an accurate estimate of the breeding population in various parts of the species' range including New Jersey.

The main goals of our study were to: (1) understand the effects of urbanization on American oystercatcher distribution at a local scale, (2) test the transferability of the MAXENT model to unsurveyed areas outside the training areas in an effort to locate new oystercatcher populations within New Jersey, and (3) evaluate the model's predictive capability using an independent dataset to validate model results. By comparing the predictions provided by our MAXENT model to the actual distribution of oystercatchers in New Jersey we hope to test the predictive capabilities of this new modeling technique in a real-world situation and further explore niche concepts in species distribution modeling.

(A) METHODS

(B) Surveys

Training data for our species distribution models were provided by two datasets of oystercatcher occurrence records (Table 1; Fig. 1). First, the New Jersey Division of Fish & Wildlife – Endangered and Nongame Species Program (ENSP) provided occurrence records for oystercatchers breeding on barrier beaches along the entire coast of New Jersey. This dataset was limited to occurrence records on the barrier beach strand since ENSP did not conduct systematic surveys for oystercatchers in alternative habitat. Second, we conducted independent surveys during 2006 for breeding oystercatchers at three study areas located in southern New Jersey that were known to have some of the highest densities of breeding oystercatchers in the state (Fig. 1). Our surveys were conducted on barrier beach strands and in all available alternative breeding habitats (i.e. saltmarsh and isolated inlet or back-bay islands) lying adjacent to the barrier islands. Surveys were conducted by walking line transects following barrier beaches and the perimeters of natural inlet islands and artificial dredge-spoil islands. We surveyed saltmarsh habitat by boat, following all navigatable shorelines and tidal creeks, and by walking line transects spaced 100 m apart. We identified all breeding pairs of oystercatchers and marked all nests/pairs located with a handheld GPS. The availability of potential oystercatcher breeding habitat types was similar at each study area.

We conducted additional surveys during 2007 to be used as an independent validation dataset to evaluate the performance of our final species distribution model (Table 1). We conducted surveys at 283 randomly selected points stratified across the range of predictive values derived by our MAXENT model output (see below). The validation surveys were conducted from May 1 to June 15, which is the peak breeding season for

oystercatchers in New Jersey. We selected random survey points in all potential oystercatcher breeding habitat (i.e. barrier beach and alternative habitats) along the New Jersey Atlantic coastline from Sandy Hook (40.48 N, -74.00 W) in the north to Cape May (38.93 N, -74.95 W) in the south, and extended 4 km inland from the Atlantic coastline. Observers recorded the presence or absence of breeding pairs of oystercatchers in a 100 m radius around each random survey point, and all breeding pairs located were marked with a handheld GPS. Most random survey points were visited once; however, we visited a subset of points (25%) twice in order to quantify detection error using an occupancy modeling technique (MacKenzie et al. 2006). This effort confirmed that a single point survey was adequate to ensure detection of breeding pairs when present.

(B) Predictive Model

We chose to use a species distribution modeling approach developed in a machine-learning environment (MAXENT software) to model oystercatcher distribution using presence-only data. MAXENT estimates a species' distribution by finding the probability distribution of maximum entropy (i.e. closest to uniform) subject to the constraint that the expected value of each environmental variable (or derived feature), and/or interactions under this target distribution, should match its empirical average (Phillips et al. 2006). MAXENT uses known occurrence records to train explanatory models (training data) and uses features composed of all pixels in the study area (background data) to predict the probability distribution over environmental space outside the training area. Recent studies have shown that MAXENT outperforms other presence-only modeling techniques (Gibson et al. 2007; Papes & Gaubert 2007; Phillips et al.

2006; Ward 2007), and performs well in comparison to a wide variety of other species distribution modeling techniques (Elith et al. 2006).

Our training data included 67 occurrence records identified during our 2006 surveys (see above), and our background data included the recommended 10,000 points drawn randomly from our 2006 study areas using Hawth's Analysis Tools for ArcGIS (version 3.26). Within our training dataset, we randomly removed all occurrence records located within 200 m of each other in order to reduce over-fitting due to spatial autocorrelation (Dormann et al. 2007). We chose this distance based on our knowledge of local oystercatcher territory sizes and to match the survey design used to collect our validation dataset. We ran our MAXENT models using the recommended default settings for maximum iterations (500), convergence threshold (10^{-5}) and regularization (1), which have been shown to improve model performance and reduce over-fitting (Phillips et al. 2006) (Dudik et al. 2007). We also selected the default "auto features" command to allow MAXENT to include the following feature types in our models, some of which are recently added extensions to the modeling software: linear, quadratic, product, threshold, hinge and discrete (Phillips & Dudik 2008). Finally, we set our model output to the default logistic output, which is considered the easiest output to conceptualize as it provides a continuous variable ranging from 0 – 1 with higher values indicating a higher probability of presence (Phillips et al. 2006).

(B) Environmental Variables

MAXENT required that we create a set of spatially explicit environmental variables as background data over which the training data was modeled (Table 2). Following the recommendations of Burnham & Anderson (2002), we selected an *a priori* set of environmental variables that we hypothesized would influence oystercatcher distribution. These variables can be grouped into three broad categories: (1) type and amount of breeding habitat available, (2) type, proximity and amount of available foraging habitat, and (3) proximity and density of urbanization. Our original set of variables included 15 variables; however, to avoid model over-fitting (Gibson et al. 2007; Rushton et al. 2004), we reduced this set to nine by removing highly correlated variables based on a non-parametric Spearman's correlation analysis (Ward 2007).

We used available land use/land cover classification data provided by the Grant F. Walton Center for Remote Sensing and Spatial Analysis (CRSSA) to derive all of our environmental variables (Table 2). We rasterized land use/land cover polygons in ArcGIS 9.2 (ESRI Inc., Redlands, CA, USA) using a 10 m cell size within an area of extent that included a 10 km buffer from the Atlantic coastline of New Jersey. All GIS-derived variables used the same cell size and area of extent, which was a requirement of the MAXENT software.

Based on distributional patterns that were apparent in our training data, we formulated the following hypotheses about the effects of our environmental variables on oystercatcher distribution:

1. Breeding oystercatchers were expected to be more abundant in alternative habitats such as saltmarsh and back-bay islands than on barrier islands.

2. The availability of sand substrates in alternative habitats was expected to have a strong positive influence on the probability of oystercatcher presence.

3. The probability of oystercatcher presence was expected to be greater in suitable breeding habitat that was in close proximity to appropriate foraging habitat. Additionally, the total area of available foraging habitat was expected to have a positive influence on the probability of presence.

4. Oystercatcher distribution was expected be clumped near Atlantic inlets since the conditions near inlets are favorable for the development of appropriate foraging habitat.

5. Oystercatchers were expected to avoid seemingly suitable breeding habitat that was in close proximity to highly urbanized areas. Further, as the density of urbanization increased the probability of oystercatcher presence was expected to decrease substantially.

MAXENT provided several outputs that offered alternative methods for analyzing the contribution of each environmental variable on the projected distribution. These included a heuristic estimate of the relative contribution that each variable had on the projected distribution and jackknife tests to examine the effects of environmental variables on the final model.

(B) Model Validation

MAXENT automatically validates model output by partitioning the training data into two sets – one that is used to train models and one that is set aside to test the models. We chose to partition 25% of the training data as test data. To evaluate model fit, we used a threshold-independent test using the area under the receiver operating characteristic (ROC) curve. The ROC curve plots model sensitivity (or true-positive rate) on the y-axis against the commission rate (1 – specificity, or false-positive rate) on the x-axis (Fielding & Bell 1997; Swets 1988). Models are evaluated based on the area under the curve (AUC), which ranges from 0 – 1. A score of one indicates perfect model discrimination, a score > 0.75 indicates good model discrimination, and a score < 0.50 indicates that the model is performing no better than random (Elith et al. 2006; Swets 1988).

While validation using data partitioned from the training data provides a useful measure of the discrimination ability of models, it is still preferable to validate models with an independent dataset whenever possible (Elith et al. 2006; Pearce & Ferrier 2000). Therefore, we performed additional analyses using validation data obtained from our independent surveys conducted in 2007 (see above). We calculated a ROC curve using the presence-absence data we collected, which allowed us to compare the AUC derived from the validation data with the AUC from the final MAXENT model. In order to calculate the ROC curve we extracted the maximum MAXENT probability value within a 110 m radius buffer around all random survey points. We chose to use the maximum MAXENT probability value in our validation since we expected oystercatcher pairs to be present if any suitable habitat was available within the 100 m survey radius.

Lobo et al. (2008) question the reliance on AUC values as the sole measure of model validation because it ignores predicted probability values, goodness-of-fit and spatial extent of the models. Thus, as a further performance test we analyzed model omission (false negative) and commission (false positive) rates separately using information provided in a confusion matrix (Anderson et al. 2003; Fielding & Bell 1997). We derived several confusion matrices using different methods to extract MAXENT values from our results, and we applied two commonly used thresholds to dichotomize the continuous distribution values (0.50 and 0.70).

(A) RESULTS

(B) Predictive Model

The MAXENT model predicted a high probability of oystercatcher presence in alternative breeding habitats removed from barrier island beaches in New Jersey (Fig. 2), especially in the southern regions of New Jersey where there is a larger amount of saltmarsh habitat available behind the barrier island complex. Results of model validation based on ROC curves generated using test data partitioned from the training data indicated that the MAXENT model performed well (Fig. 3), exhibiting good discrimination ability based on analyses of both the training data (AUC = 0.95) and test data (AUC = 0.91). The MAXENT model provided predictions that were useful to locate new oystercatcher populations. Ground surveys based on our model located 185 previously unknown breeding pairs of oystercatchers in coastal New Jersey.

(B) Explanatory Variables

The heuristic estimates (Table 2) indicated that distance from tidal waters had the greatest influence on predicted oystercatcher distribution with probability of presence substantially higher in areas closer to tidal waters. The heuristic estimate also indicated that habitat type had a very large influence on predicted oystercatcher distribution. The response curve for the habitat classification variable indicated oystercatchers used low marsh (*Spartina alterniflora* dominant marsh), vegetated dunes, barrier beaches and other beaches including those found on inlets, natural or artificial islands and saltmarsh margins. Sandy beaches found in alternative habitat had by far the highest probability of oystercatcher presence, as we hypothesized. While the availability of sand substrates appeared to increase the probability of oystercatcher occurrence, nests found in alternative habitat during our 2007 validation surveys ($N = 103$) were placed on both sand substrate ($N = 51$) and wrack deposits ($N = 53$). Examination of the jackknife tests of training and test gains confirmed that the most important contributing variables in the final MAXENT model were distance from tidal waters and habitat type (Fig. 4).

Further examination of the jackknife test of AUC indicated that several variables were more important contributors to the final MAXENT model than indicated by the heuristic estimate. These variables included three that were related to the amount of foraging habitat available both in close proximity to potential nest sites (within 100 m) and distant from nest sites (within 1 km). This supports our hypothesis that oystercatchers select breeding habitat in close proximity to foraging areas. The jackknife test of AUC also indicated that the probability of oystercatcher presence was influenced to some degree by

the amount of urbanization within 1 km of potential breeding areas with a much lower probability in highly developed areas.

(B) Model Validation

Results of independent oystercatcher surveys conducted along the New Jersey Atlantic coastline during 2007 indicated that most breeding oystercatchers were distributed in alternative habitats as the MAXENT model suggested (Table 1; Fig. 5). Nevertheless, the ROC curve generated for our independent validation data indicated that the MAXENT model did not perform much better than random (AUC = 0.54). Further, the AUC for our validation data was well below the AUC for the final MAXENT model (AUC training data = 0.95) indicating poor validation of the model.

In order to further examine the source of errors in our MAXENT model, we isolated errors of omission and commission by analyzing observed and predicted presence/absence patterns of our independent validation data in confusion matrices (Table 3). These matrices indicated that there was a high omission error rate (0.76 – 0.93) regardless of method or threshold used to derive the error rate. The commission error rate was also high (0.74 – 0.83) when a 0.50 threshold was used to derive the rate; however, the rate was lower (0.40 – 0.69) when a 0.70 threshold was used.

(A) DISCUSSION

The maximum entropy modeling technique that we employed provided valuable information regarding the distribution of American oystercatchers in New Jersey's highly

urbanized coastal ecosystem. At a regional scale (statewide), the MAXENT model accurately predicted a higher probability of oystercatcher presence in alternative breeding habitats away from the barrier beach strand, which is the preferred breeding habitat for the species. Ground surveys based on our model located 185 previously unknown breeding pairs of oystercatchers in alternative habitats in coastal New Jersey, which more than doubled the estimate of the local breeding population. As a result of our surveys, we now estimate that 81% of the New Jersey oystercatcher population breeds in alternative habitats away from the barrier beach strand.

The models also showed that oystercatchers were less likely to be found in areas with a high degree of urbanization. This pattern may partially explain the low predictive values reported in the northern part of the New Jersey coast, which is the most highly developed coastal area in the state. In addition, the amount of coastal development limits the total area of suitable breeding habitat in the region to small, fragmented patches. For example, the habitat surrounding Barnegat Bay has been severely altered with over 70% of the adjacent upland shoreline developed and 36% of the total shoreline bulkheaded (Lathrop & Bognar 2001). This activity limits the amount of alternative breeding and foraging habitat available to oystercatchers in this region. At the local scale, oystercatchers had a much higher probability of presence in alternative breeding habitats where sand was available as a nesting substrate, although wrack deposits were also used regularly for nest placement in these habitats. Thus, the realized niche of the American oystercatcher in New Jersey is predicted to be alternative breeding habitats such as saltmarsh, inlet or back-bay islands that have exposed sand available as a nesting substrate.

Based on this visual interpretation of our model results, the MAXENT model performed well at the regional scale and the predictions appear to be very transferable to areas outside the training area. However, at the local scale, we saw that the predictive capability of the final MAXENT model was poor. Regardless of the method used to analyze the final model with our independent validation dataset, AUC values were below those necessary to indicate good model discrimination and omission errors were unacceptably high. However, validation of models in this manner is expected to be difficult due to the incomplete information that is used to develop distribution models (Fielding 2002), and it may even be conceptually impossible to perfectly validate models in this manner (Araujo et al. 2005). There are a number of potential explanations as to why we did not see a strong validation of the MAXENT model using the independent validation dataset including: (1) over-fitting of models, (2) data errors in predictive models and (3) models accurately predict the realized niche but oystercatchers are utilizing unsuitable (sink) habitat. We explore each of these potential explanations for the weak model validation below.

The first two explanations deal with possible errors in the construction of our MAXENT model. First, the high omission error rate (0.76 – 0.93) of our validation data indicates that oystercatchers are occurring in high numbers in areas not predicted by the distribution model. This result could indicate that the MAXENT model is over-fit, thus seriously under-predicting the amount of suitable breeding habitat that is available. However, we took measures to reduce this potential error in the model-building process

by addressing issues known to cause over-fitting such as spatial autocorrelation of occurrence records, multi-collinearity of environmental variables, and using excess predictor variables with small training datasets. Further, over-fitting is prevented in the MAXENT software by the regularization and feature selection processes used in the algorithms (Dudik et al. 2007). As such, we do not feel that over-fitting is a good explanation for the poor model validation.

Second, it is possible that there were errors in the background GIS data used to construct our environmental layers. Ground-truthing of habitat features at random survey points, which was performed during our surveys, revealed some classification errors in the GIS data. For example, we identified several areas where small sandy margins in saltmarsh habitat were not classified properly in our GIS layers; therefore, these areas would have received higher predicted suitability values in our final model. The occurrence of oystercatchers in these areas led to misclassified false negatives in our confusion matrices. Correction of these misclassifications would lower the omission error rate to some degree; however, there were few errors of this type identified. Therefore, the omission error rate would still be extremely high even if we corrected for these errors.

In the absence of data errors in our models it is possible that the final model accurately predicts the realized niche, but oystercatchers are utilizing unsuitable (sink) habitat. The goal of our distribution model was to predict the realized niche of the species, and we expected the actual distribution to overlap this niche due to the dispersal ability of the species, keeping in mind that a good model of a species' niche may not necessarily

coincide with the current distribution of that species (Phillips 2008). The MAXENT model predicted the realized niche (highly suitable areas) well, supported by the observation that these areas had much higher densities of breeding pairs (T. Virzi, personal observation). However, our independent surveys indicated that oystercatchers were also widely distributed in areas predicted to be unsuitable.

Metapopulation theory indicates that species will be distributed across a range of habitat suitability rather than just in highly suitable areas (Morin 1999). Source-sink dynamics further predict that a species will often occupy seemingly unsuitable habitat in high density, especially when dispersal ability is strong (Pulliam 1988, 2000). A highly mobile species such as the American oystercatcher could be expected to show this pattern. In fact, Ens (1992) showed a despotic distribution for the European oystercatcher where individuals often attempted to breed in less suitable habitat, hypothesized to be due to intense intra-specific competition for the most suitable (and most productive) habitat. Further, many individuals also chose not to breed at all and waited in queue for an opening in the most suitable habitat.

By comparing maps of the MAXENT predictions (Fig. 2) with the actual distribution (Fig. 5), it is clear that oystercatcher occurrences in unsuitable habitat are often located near areas with high suitability values. We interpret this as evidence that oystercatchers in New Jersey are exhibiting a similar despotic distributional pattern as reported for the European oystercatcher. Our study of oystercatcher nest success (Chapter 1) showed that most oystercatcher productivity in New Jersey comes from the areas predicted to be most

suitable by the MAXENT model; therefore, these areas may be acting as sources for the local population. Further, low-lying saltmarsh areas, which are predicted as unsuitable by the MAXENT model, exhibit poor nest productivity indicating these areas may be acting as sink habitat. The high density of breeding pairs in areas with high suitability values may also indicate that these areas are saturated with oystercatchers, forcing many individuals to breed in nearby low-lying saltmarsh sink habitat. Given the condition of coastal ecosystems in New Jersey it is not surprising that such a high proportion of the known oystercatcher population (69%) occurs in unsuitable (sink) habitat.

The high commission error rate (0.40 – 0.83) of our validation data indicates that our MAXENT model did not predict oystercatcher presence well, even in habitat that was predicted to be highly suitable. This suggests that there may be additional factors not included in our models that may be further influencing the local oystercatcher distribution. It is possible that human disturbance on breeding grounds, which was not included in our models, may be keeping oystercatchers from utilizing highly suitable breeding habitat. Persistent human disturbance on or near breeding grounds is known to affect settlement and territory establishment of birds, causing birds to abandon optimal habitat and subsequently settle in sub-optimal habitat (Erwin 1980; Van der Zande & Vestral 1985; Yalden & Yalden 1990).

The small number of potential source populations breeding in highly suitable habitat in New Jersey does not bode well for the viability of the state's oystercatcher population. More importantly, the distributional patterns reported in New Jersey are repeated in other

urbanized ecosystems such as in Maryland, where approximately 89% of the known oystercatcher population breeds in alternative habitats (Traut et al. 2006). There could be severe consequences to the overall Atlantic coast oystercatcher population if the species is indeed expanding its range northward and concurrently shifting its breeding habitat into sink habitat. Further research is needed to understand oystercatcher productivity in alternative breeding habitats and to identify small, isolated areas that may act as local source populations. Furthermore we recommend that surveys based on predictions in a distributional model should be designed so that sink populations may also be located. This can be achieved by having a survey design that includes searches in both highly suitable habitat and adjacent unsuitable habitat where sink populations might be expected.

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(A) TABLES

Table 1 Summary of all occurrence records used as training data in our species distribution models and pooled survey data for New Jersey. Training data are all occurrence records identified during 2006 surveys at select study areas. Survey data are all occurrence records identified during 2007 independent surveys at/near randomly selected points along the New Jersey coastline (within a 4 km buffer from Atlantic coastline) pooled with 2007 survey data at training areas, which represents the total known oystercatcher population in the state.

	Training Data		Survey Data	
Habitat Type	No. Pairs	% Total	No. Pairs	% Total
Barrier Beach	38	56.7%	60	19.4%
Saltmarsh	22	32.8%	213	69.0%
Inlet Islands	3	4.5%	10	3.2%
Dredge-Spoil Islands	4	6.0%	26	8.4%
Total	67	100.0%	309	100.0%

Table 2 Description of environmental variables used in MAXENT models
and a heuristic estimate of the relative contribution of each environmental
variable on the projected distribution, as provided by MAXENT output.

Description[1]	% Contribution
Distance from nearest tidal waters	46.8%
Habitat classification	33.3%
Distance from nearest inlet	10.9%
Area of low marsh edge within 100 m radius	3.6%
Area of tidal flats within 1 km radius	1.7%
Area of urbanization within 100 m radius	1.6%
Area of tidal flats within 100 m radius	1.6%
Area of low marsh edge within 1 km radius	0.4%
Area of urbanization within 1 km radius	0.1%
Total Contribution	100.0%

[1]Distance variables measured as Euclidean distances using nearest neighbor
function; area variables calculated as focal statistics using a 10 x 10 m moving
window within a radius of either 100 m or 1 km surrounding all pixels in the
area of extent; all calculations done with Spatial Analysis Tools in ArcGIS
9.2; all variables continuous except habitat classification which is categorical

Table 3 Confusion matrices and error rates derived from presence/absence data collected during 2007 oystercatcher surveys. Matrices based on three methods used to extract MAXENT probability values and two thresholds.

Measure[3]	Threshold[4]	Validation Data[1,2] AUC$_{max}$ = 0.54					
		TP	FN	TN	FP	OE	CE
Point	0.50	9	37	203	34	0.80	0.79
Mean	0.50	6	40	220	17	0.87	0.74
Max	0.50	11	35	185	52	0.76	0.83
Point	0.70	6	40	230	7	0.87	0.54
Mean	0.70	3	43	235	2	0.93	0.40
Max	0.70	8	38	219	18	0.83	0.69

[1]Confusion matrices based on presence/absence data at random survey points; AUC$_{max}$ = area under the ROC curve based on maximum MAXENT probability value within 110 m radius of points

[2]TP = true positives, FN = false negatives, TN = true negatives, FP = false positives, OE = omission error rate [FN / (FN + TP)], CE = commission error rate [FP / (FP + TP)]

[3]Methods used to derive confusion matrices: Point = point values, Mean = mean values within 110 m radius, Max = maximum values within 110 m radius

[4]Thresholds used to dichotomize continuous distribution values

(A) FIGURE LEGENDS

Figure 1   Oystercatcher occurrence records used as training data in our species distribution models. The three high density breeding areas where we conducted intensive surveys in alternative breeding habitat are identified and include: (1) the Southern Natural Area of Island Beach State Park (IB) located in Ocean County, New Jersey (39.77 N, -74.10 W), (2) the Holgate Division of the Edwin B. Forsythe National Wildlife Refuge (HG) also located in Ocean County (39.50 N, -71.30 W), and (3) Stone Harbor Point (SH) located in Cape May County (39.03 N, -74.78 W). The habitat available for breeding oystercatchers at IB includes 3.3 km of undeveloped barrier beach, a 1.6 km artificial inlet beach along an artificial dike, approximately 197 hectares of adjacent saltmarsh, and an 8 hectare artificial dredge-spoil island located in Barnegat Bay. The habitat available for oystercatchers at HG includes 6.0 km of undeveloped barrier beach, approximately 74 hectares of saltmarsh located directly adjacent to the barrier beach strand, and a 5 hectare naturally-forming inlet island located within Little Egg Inlet. The habitat available for oystercatchers at SH includes 1.8 km of partially developed barrier beach, approximately 23 hectares of saltmarsh located directly adjacent to the barrier beach strand, a 126 hectare nearby saltmarsh island, and an 11 hectare naturally-forming inlet island located within Hereford Inlet.

Figure 2 Predicted MAXENT distribution displayed using a color ramp of probability values ranging from 0 (blue) – 1 (red). Predictive maps were masked by New Jersey county boundaries to show the change in predicted oystercatcher distribution moving from north to south along the Atlantic coastline.

Figure 3 Receiver operating characteristic (ROC) curves for training, test and independent validation data used to evaluate the MAXENT distribution model. ROC curves for training and test data provided by MAXENT output. ROC curve for our independent validation dataset calculated using JMP software version 7.0 (SAS Institute, Cary, NC, USA) based on maximum MAXENT probability value and presence/absence data collected within a 110 m buffer around random survey points.

Figure 4 Jackknife tests of training gain (gain is related to deviance), test gain and AUC for the MAXENT model. Models run by removing each variable individually do not improve the gain substantially above the overall gain of the MAXENT model based on training data with the exception of distance from inlets, indicating all variables contribute to the distribution to some degree. Models run with each variable in isolation indicate that habitat type has the most useful information by itself. The jackknife of AUC indicates that habitat type, distance from tidal waters, and amount of saltmarsh habitat in close proximity to potential breeding areas (i.e. within 100 m) achieve good amounts of discriminating ability (AUC > 0.75) when looked at in isolation. Other variables that gain importance in the jackknife of AUC include amount of saltmarsh and tidal flats

distant from potential breeding areas (i.e. within 1 km) and amount of urbanization within 1 km of breeding areas.

Figure 5   New Jersey oystercatcher distribution based on results of 2007 surveys conducted within a 4 km buffer from the Atlantic coastline. Data presented includes all breeding pairs located during independent surveys including those found within a 110 m buffer around random survey points, those found incidentally while traveling between random survey points, and all pairs identified during concurrent censuses at training areas.

(A) FIGURES

Figure 1

Area of detail: example oystercatcher distribution at select study site (IB)

Figure 2

MAXENT Probability of Occurrence
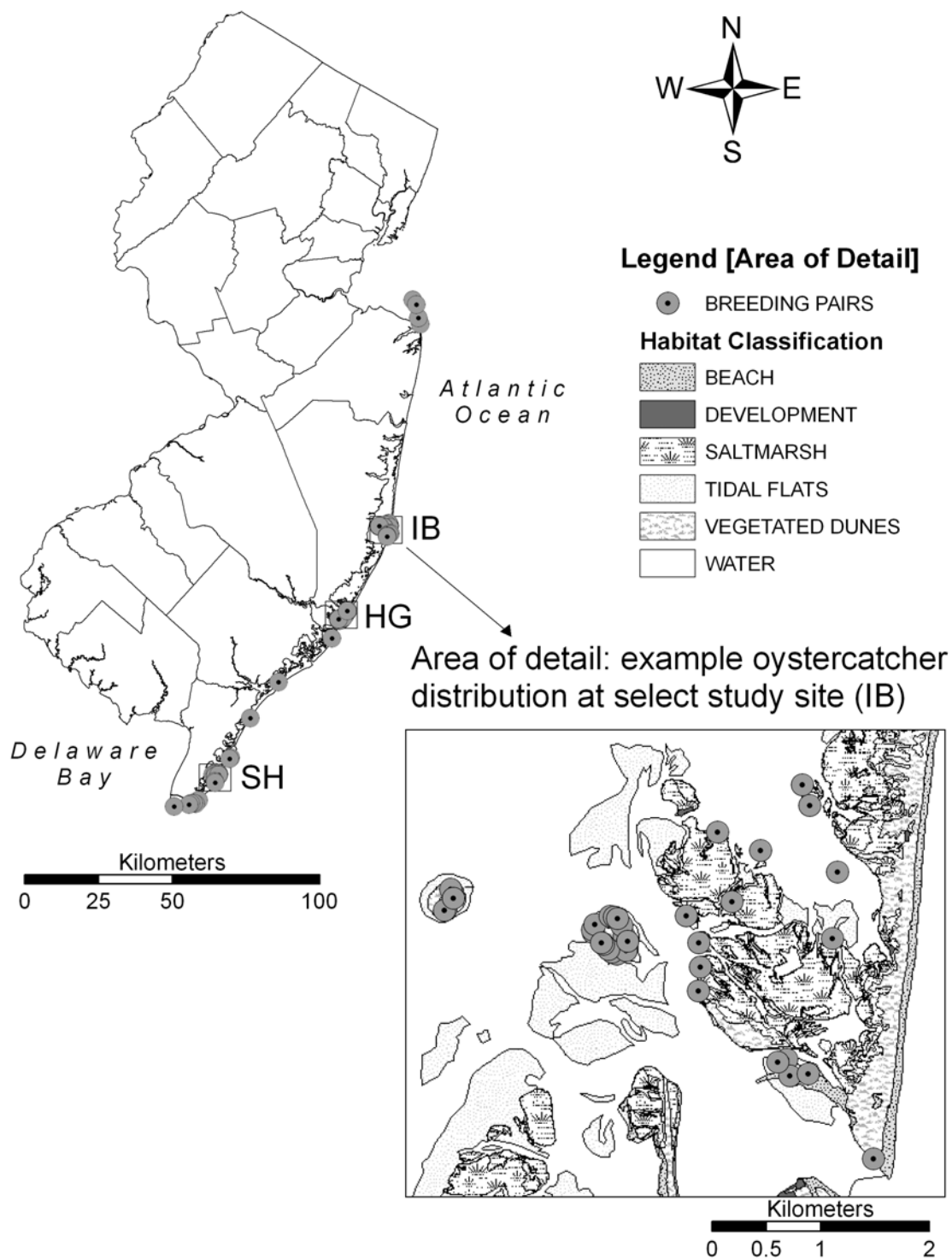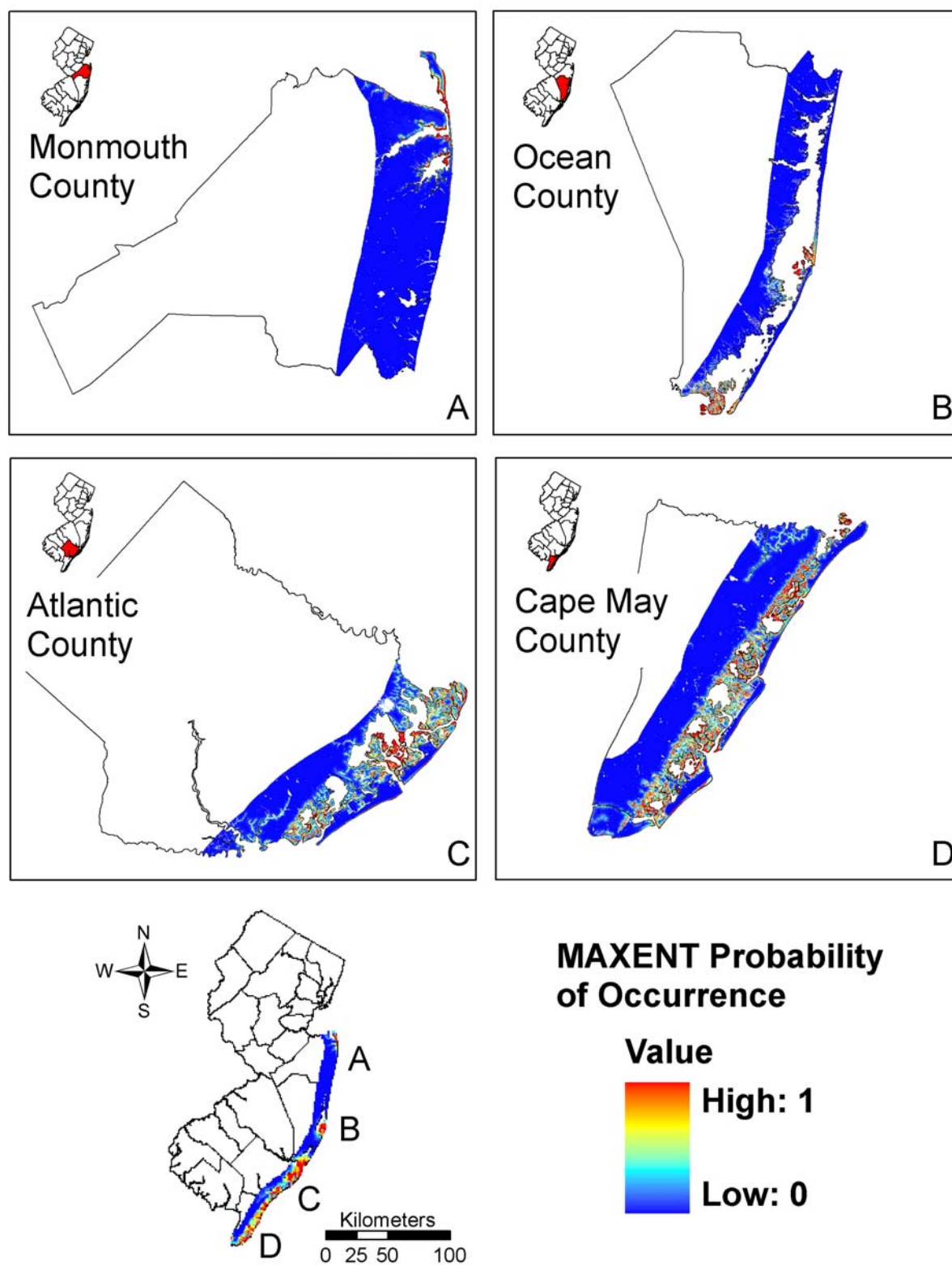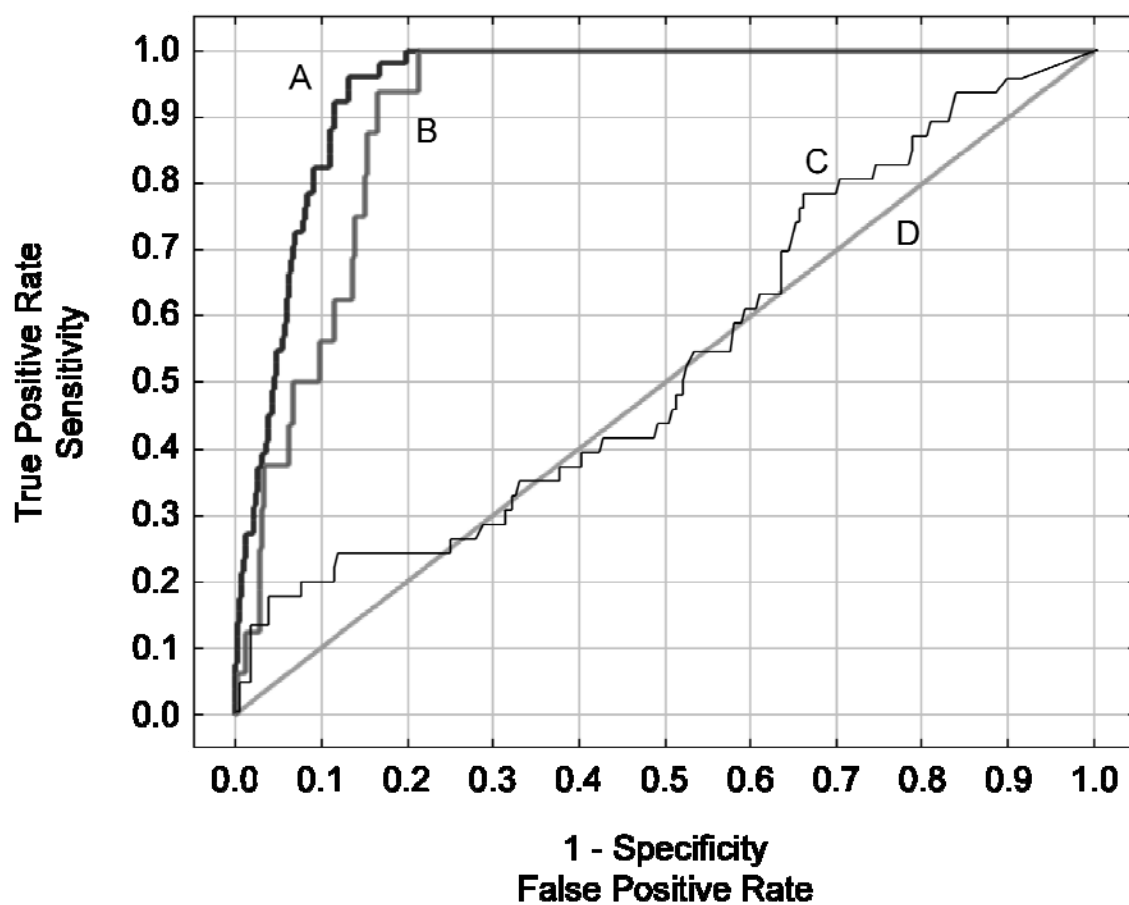
Figure 3

A - Training Data   (AUC = 0.947)
B - Test Data   (AUC = 0.911)
C - Validation Data   (AUC = 0.536)
D - Random Prediction   (AUC = 0.500)

Figure 4
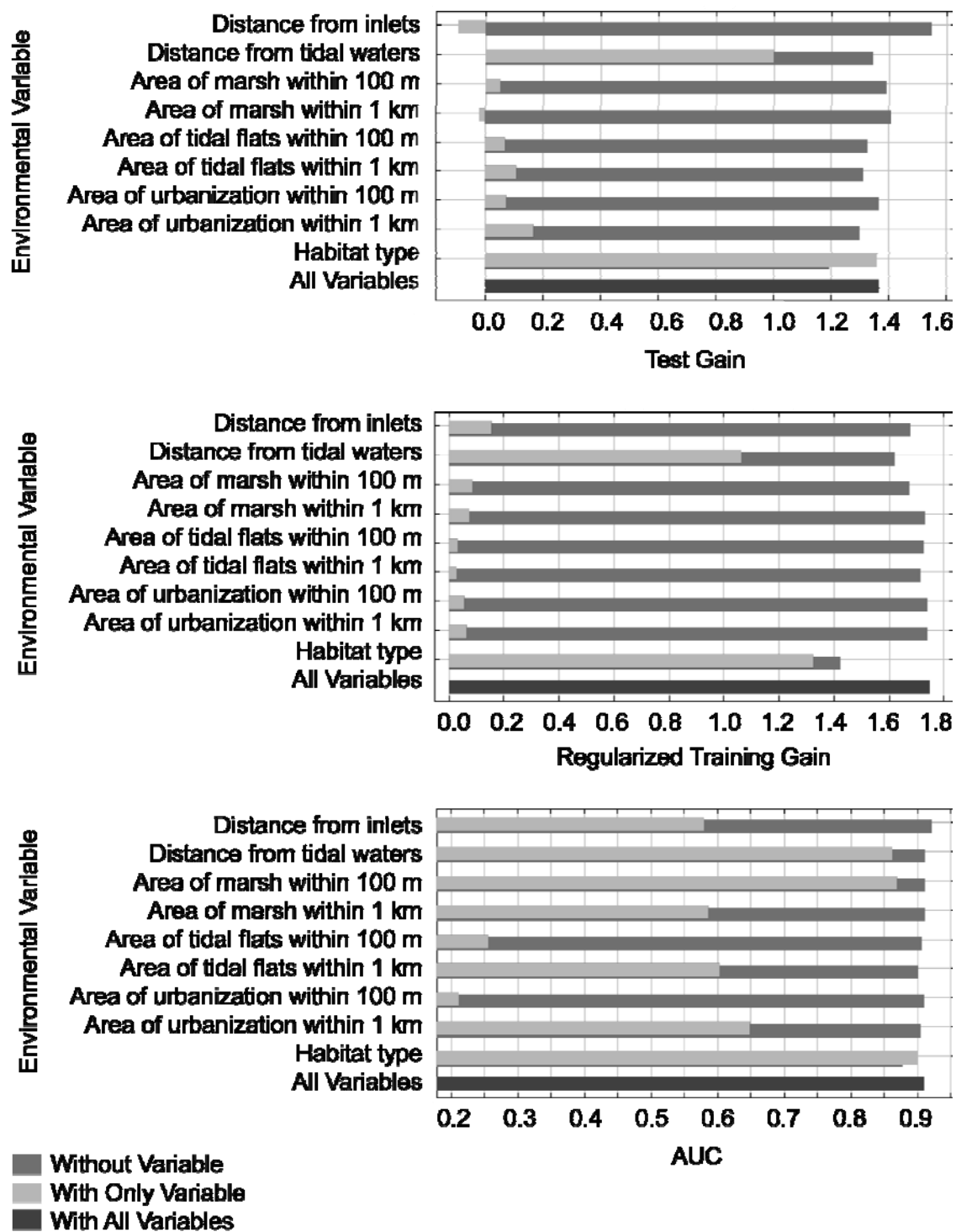
Figure 5
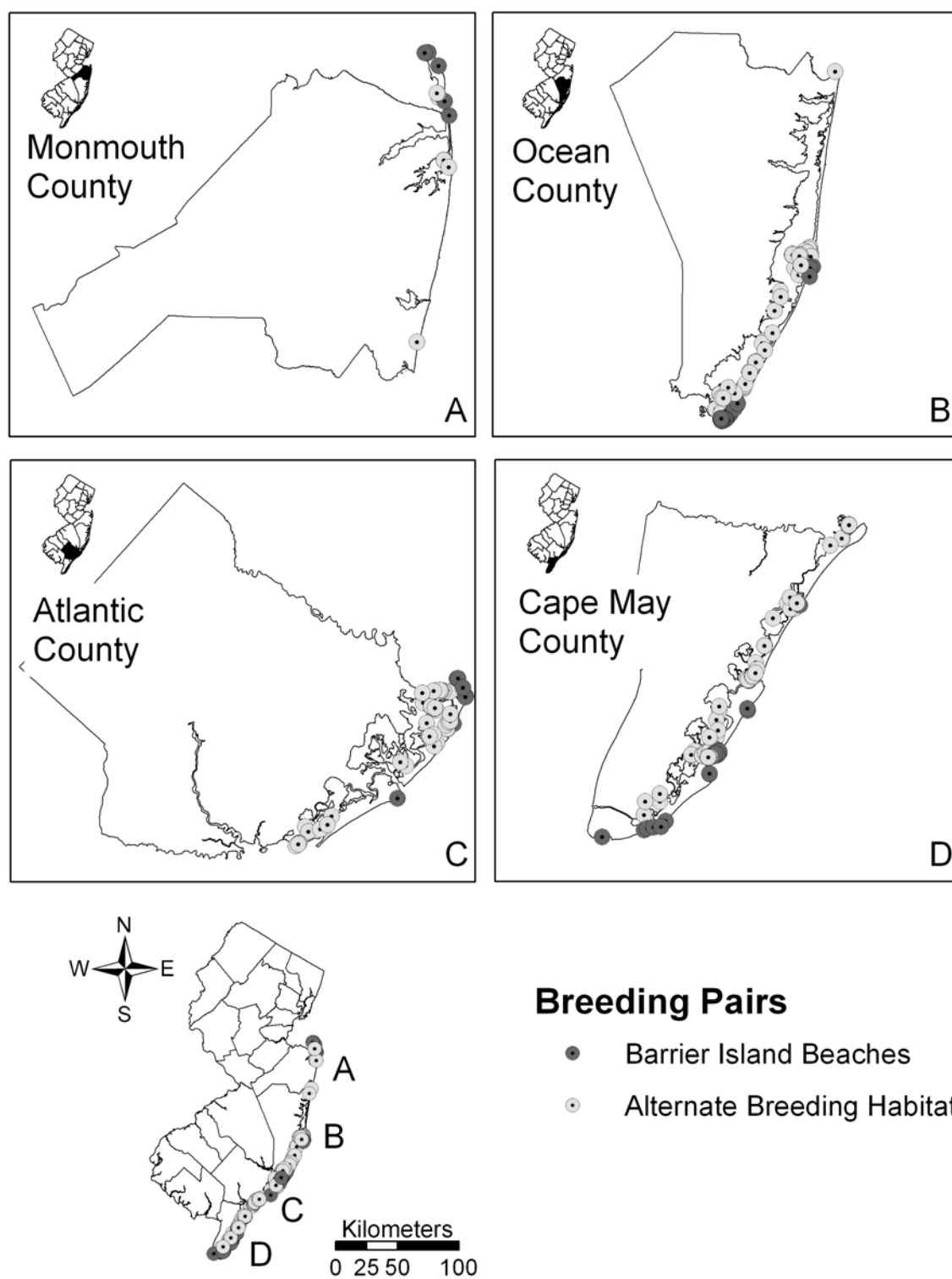
Breeding Pairs

• Barrier Island Beaches

⊙ Alternate Breeding Habitat

CHAPTER 3

The Effect of Human Disturbance on the Local Distribution of American Oystercatchers Breeding on Barrier Island Beaches

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ABSTRACT

On the barrier beaches of New Jersey, there is a high intensity of recreational activity that coincides with the breeding season for many beach-nesting birds, including the American oystercatcher. Persistent human disturbance on or near breeding grounds could affect settlement and territory establishment of birds, causing them to abandon optimal habitat and subsequently settle in sub-optimal habitat. Explaining the distributional variation in response to human disturbance pressure is difficult; however, there are many recently developed species distribution modeling techniques that perform well for such analyses. We used classification and regression tree models to identify the most important variables explaining the distribution of American oystercatchers in response to recreational activity in a highly disturbed coastal ecosystem, and compared the models with other more complex techniques. The classification and regression tree models performed well, and

were the easiest models to implement and interpret making them an ideal choice for such analyses. Our results indicated that human disturbance affects the local distributional patterns of American oystercatchers on New Jersey barrier beaches. Probability of oystercatcher presence was lower on highly disturbed beaches and in areas that were in close proximity to access points. Further, there was lower probability of presence on beaches that permit driving during the month of May, which is the peak nest-initiation period for oystercatchers in the region. Probability of American oystercatcher presence and abundance were greatest in highly suitable barrier beach habitat that had a low level of human disturbance. Therefore, we suggest that restrictions be placed on beach access and driving during the key breeding season on beaches that are predicted to be highly suitable for oystercatcher nesting.

Keywords

American oystercatcher, classification and regression trees, maximum entropy modeling, random forests, recreational disturbance, species distribution modeling

INTRODUCTION

American oystercatchers (*Haematopus palliatus palliatus*) face significant threats throughout their range including habitat loss, habitat degradation, potential prey resource depletion, increasing threats from predators and human disturbance (Brown et al. 2005). Historically, the preferred breeding habitat for American oystercatchers was barrier beach habitat. However, barrier beaches in many parts of the species' range, including in New Jersey, have been severely degraded by extensive coastal development, beach stabilization practices and high levels of recreational disturbance. New Jersey is the most densely populated state in the United States, and the population in coastal counties swells during the summer months as tourists flock to local beaches. The state's beaches are in close proximity to major metropolitan areas including New York City, which is the third most populated coastal city in the world (Martinez et al. 2007). Thus, there is an intensification of recreational activity that coincides with the peak breeding season for many beach-nesting birds, including the American oystercatcher. At present, we do not have a clear understanding of the effects of high levels of human disturbance on oystercatcher distribution in urbanized coastal ecosystems such as those found in New Jersey. We used novel species distribution modeling techniques to show that oystercatcher distribution is influenced by human disturbance.

Human disturbance on breeding grounds can affect the reproductive success of birds in a variety of ways during different phases of the reproductive cycle including alteration of nest-site selection, abandonment of nesting territories, disruption of incubation, increased

predation, thermal stress on eggs and chicks, disruption of foraging and increased energy expenditures by adults and fledglings (Burger 1991; Carney & Sydeman 1999; Erwin 1980; Flemming et al. 1988; Gill et al. 1996; Major 1990; Safina & Burger 1983; Van der Zande & Vestral 1985; Yalden & Yalden 1990). Human disturbance has been linked to a reduction in reproductive success in several oystercatcher species including the African black oystercatcher (*H. moquini*) (Leseberg et al. 2000), the European oystercatcher (*H. ostralegus*) (Verhulst et al. 2001) and the American oystercatcher (McGowan & Simons 2006), and may have contributed to the extinction of the Canarian black oystercatcher (*H. meadewaldoi*) (Hockey 1987).

Human development and persistent human disturbance on or near breeding grounds early in the breeding season could affect settlement and territory establishment of birds, causing birds to abandon optimal habitat and subsequently settle in sub-optimal habitat (Erwin 1980; Van der Zande & Vestral 1985; Yalden & Yalden 1990). Shorebirds may be particularly vulnerable to the effects of disturbance on breeding grounds (Cardoni et al. 2008), with the consequence often being that individuals are displaced from the best habitat (Lafferty et al. 2006; Schulz & Stock 1993). High levels of human disturbance on beaches cause oystercatchers and other shorebirds to breed in greater numbers in alternative habitats (Colwell et al. 2005; McGowan et al. 2005; Toland 1999). Thus, the high level of recreational disturbance on New Jersey's barrier beaches may explain the high proportion of American oystercatchers breeding in alternative habitats (Chapter 2).

Explaining the distributional variation in response to human disturbance pressure is difficult; however, there are many recently developed species distribution modeling techniques that perform well for such analyses. Ecological data are often complex and unbalanced, often violating the assumptions necessary to use parametric statistics to describe relationships without transforming data (De'Ath & Fabricius 2000). Species distribution modeling techniques use nonparametric tests to examine complex relationships between occurrences and environmental variables. One such technique that has seen widespread use in ecological applications is classification and regression tree (CART) modeling (Breiman et al. 1998). CART models have been used for a wide range of applications such as explaining the response of environmental variables on species distributions, predicting the location of new populations, identifying variables contributing to the establishment of invasive species and examining the effects of urbanization on distributions (Bourg et al. 2005; Palomino & Carrascal 2007; Usio et al. 2006; Zigler et al. 2008). We used CART models to identify the most important variables explaining the distribution of American oystercatchers in response to recreational activity.

There are a number of other species distributional modeling techniques that have been used in recent decades such as generalized additive models (Guisan et al. 2002), multivariate adaptive regression splines (Munoz & Felicisimo 2004), boosted regression trees (De'Ath 2007), random forests (Cutler et al. 2007) and maximum entropy models (Phillips et al. 2006). These complex modeling techniques are often used to predict the fundamental niche of a species at broad scales (e.g. continental scale) using

environmental variables such as temperature, precipitation or elevation (Phillips et al. 2006). However, these models may also be used to predict the realized niche at a smaller scale if predictor variables such as substrate type are included (Karl et al. 2000). The actual distribution of a species, however, will often be different than the realized niche at local scales (Pulliam 2000). At the local scale, factors such as inter-specific competition and human disturbance also play important roles in affecting species distributions (Thuiller et al. 2004). To date, few species distribution models have incorporated human disturbance layers as explanatory variables, although recent studies show that species distributions are indeed affected by such variables (Agness et al. 2008; Lippitt et al. 2008).

Here, we develop and compare simple CART models with other more complex species distribution modeling techniques. In Chapter 2, we modeled the realized niche of the American oystercatcher in New Jersey based on environmental variables and the extent of urbanization. Our species distribution model performed well at a regional scale; however, the model had poor predictive power at a local scale when validated with an independent dataset based on ground surveys. The actual distribution showed that a high proportion of oystercatchers (69%) nested in sink habitat, and we hypothesized that this was partially due to the severely limited amount of highly suitable breeding habitat that remains in New Jersey. However, there is still available habitat on the state's barrier beaches predicted to be highly suitable that is not being used by oystercatchers. For a species going through a range expansion such as the American oystercatcher, highly suitable habitat that is unsaturated should be filled first before any shift into alternative

habitat (Fielding & Bell 1997). Here, we hypothesize that oystercatchers in New Jersey are being displaced from the remaining highly suitable habitat on barrier beaches due to high levels of human disturbance.

The main goals of our study were to: (1) determine if human disturbance affects oystercatcher distribution, (2) analyze the effects of various types and levels of human disturbances on the local distribution, and (3) compare the performance of CART models to other more complex species distribution modeling techniques.

METHODS

Training Data

We used presence and absence records as training data for our species distribution models. These data were provided by ground surveys conducted during 2007 along all Atlantic Ocean-facing barrier beaches in New Jersey from Sandy Hook (40.48 N, -74.00 W) to Cape May (38.93 N, -74.95 W) (see Chapter 2 for methods). Breeding pairs of oystercatchers were located and marked with a handheld global positioning system device (Garmin eTrex Vista, accuracy < 5 m) for later integration into a geographic information system. We identified 68 occurrence records during the surveys for use as presence data in our models. We also included 68 absence records in our models; absence was confirmed based on visits to randomly selected points within the study areas.

For all training data points we recorded the total number of breeding pairs located within a 100 m radius surrounding the point for analysis of abundance in regression tree models.

Explanatory Variables

Our distribution modeling techniques required the creation of a set of explanatory variables that were used in a spatial context as background data over which the distribution of presence and absence records were modeled (Table 1). In Chapter 2, we identified a suite of regional-scale environmental variables that were used to model habitat suitability for oystercatchers using a maximum entropy modeling approach. The resulting model provided a map of habitat suitability values (or probability distribution) for all pixels in the study area. We extracted these values to the training data points using Hawth's Analysis Tools (version 3.26) for ArcGIS 9.2 (ESRI, Inc., Redlands, CA, USA). Thus, the first explanatory variable in our species distribution models was the probability of oystercatcher presence, which excluded additional explanatory variables for human disturbance.

The remaining explanatory variables examined the effects of human disturbance on oystercatcher distribution. Following the recommendations of Burnham & Anderson (2002), we selected an *a priori* set of explanatory variables that we hypothesized would influence oystercatcher distribution at a local scale. Thus, we chose six additional explanatory variables related to recreational disturbance on barrier beaches (Table 1).

We kept the number of explanatory variables low because using excess variables with small training datasets is known to cause over-fitting of models (Gibson et al. 2007; Rushton et al. 2004).

We formulated the following hypotheses about the effects of the selected explanatory variables on the local distribution of oystercatchers on New Jersey barrier beaches:

1. Oystercatchers were expected be more abundant in areas with high habitat suitability values.

2. Oystercatchers were expected to be less abundant in highly suitable areas when the level of human disturbance was high.

3. Driving on beaches during the breeding season should displace oystercatchers from suitable habitat.

4. We expected temporal variation in the effects of driving on oystercatcher distribution, with the most severe effects occurring during the peak nest initiation period (late-April through May).

Modeling Techniques

We used several modeling techniques to test the efficacy of CART models compared to more complex distributional modeling techniques. One of the main advantages of CART modeling is the ease of interpretation of the results (De'Ath & Fabricius 2000). The main purpose of our analyses was to determine the most important explanatory variables

affecting oystercatcher distribution in response to recreational disturbance. Each of the modeling techniques provided an estimate of variable contributions, and these were compared between models. The benefit of using several different modeling techniques is that models may be evaluated against each other, lending support to interpretations of any single model.

First, we used CART models to examine the effect of human disturbance on oystercatcher distribution. Although easy to use, CART models perform well compared to other more advanced modeling techniques (Munoz & Felicisimo 2004; O'Brien et al. 2005; Turgeon & Rodriquez 2005). CART models explain the variation of a single response variable by repeatedly splitting the data into more homogeneous groups based on multiple explanatory variables (De'Ath & Fabricius 2000). The response variable in classification tree analysis is presence or absence of the species, while the response variable in regression tree analysis is species abundance. In both analyses, the first step is to grow an overlarge tree by splitting the tree into many branches using a simple decision rule that partitions the data into two mutually exclusive groups at each node (split) of the tree. The decision rule for classification trees is to select the split that minimizes the misclassification rate at each node. For regression trees, splits minimize the sum of squares about the group mean at each node. The overlarge tree is then pruned back based on a v-fold cross-validation process resulting in the tree that explains the minimum error. The best tree is determined using the 1-SE rule, or the most parsimonious tree that is within 1-SE of the tree with the minimum error (Breiman et al. 1998).

We used CART software version 6.0 (Salford Systems, San Diego, CA, USA) for all CART analyses. In all models, we used the Gini index for measuring the homogeneity of nodes, allowed surrogate values for missing explanatory variables, and used a 10-fold cross-validation process. We determined the final tree size in each analysis by examining a series of 50 cross-validations so that we could assess the variation in the size of the best tree selected in each run, ensuring that the size of the selected trees were not atypical (De'Ath & Fabricius 2000).

Second, we modeled the species distribution with a classification technique that is well established in other fields but is rarely used in ecology, random forests modeling (Cutler et al. 2007). This technique is based on classification trees; however, rather than building a single best tree this technique constructs a series of trees and combines the predictions to explain the distribution. Recent studies show that ensemble methods such as random forests may provide better prediction accuracy (Berk 2006; Cutler et al. 2007; Prasad et al. 2006). The random forests technique generates more accurate predictions by introducing two types of randomization into the model building process. First, randomized bootstrap samples are drawn from the training data to construct multiple trees. Second, each tree is grown with a randomized subset of the explanatory variables.

We used RandomForests software version 1.0 (Salford Systems, San Diego, CA, USA) for all random forests analyses. We ran our random forest models using the default settings of 500 bootstrap samples, three terminal nodes per tree, and the standard error

method for validating trees. We set aside 25% of the training data from the bootstrap samples for out-of-bag observations used to validate the models based on classification accuracy rates.

Finally, we used a species distribution modeling approach developed in a machine-learning environment (MAXENT) to model local oystercatcher distribution in response to human disturbance (Phillips et al. 2006). MAXENT estimates a species' target probability distribution by finding the probability distribution of maximum entropy (i.e. closest to uniform), subject to the constraint that the expected value of each environmental variable (or derived feature) and/or interactions under this target distribution should match its empirical average (Phillips et al. 2006). MAXENT ordinarily uses presence-only data to train the explanatory models; however, absence data may be incorporated into the training data to predict the probability distribution (Phillips et al. 2006).

We used MAXENT software version 3.2.1 to run our maximum entropy models, which is freely available for download (http://www.cs.princeton.edu/~schapire/maxent). We ran our MAXENT models using the recommended default settings for maximum iterations (500), convergence threshold (10^{-5}) and regularization (1), which have been shown to improve model performance and reduce over-fitting (Dudik et al. 2007; Phillips et al. 2006). The final MAXENT model was validated by setting aside 25% of the training data as test data and comparing predictions using the area under the receiver operating characteristic (ROC) curve.

Model Comparison

In order to compare the overall performance of the different classification models, we used a threshold-independent test examining the ROC curves for each model. The ROC curve plots model sensitivity (or true-positive rate) on the y-axis against the commission rate (1 – specificity, or false-positive rate) on the x-axis (Fielding & Bell 1997; Swets 1988). Models are evaluated based on the area under the curve (AUC) which ranges from 0 – 1, where a score of one indicates perfect model discrimination, a score > 0.75 indicates good model discrimination, and a score < 0.50 indicates that the model is performing no better than random (Elith et al. 2006) (Swets 1988). The use of AUC to validate models is preferable since it takes into consideration all of the information included in the classifiers and allows easy comparison between models (Fielding & Bell 1997).

RESULTS

CART Models

The classification tree model performed well, exhibiting good discrimination ability (AUC = 0.93). The final classification tree had seven terminal nodes (Fig. 1). Selection

of the final tree size was based on the modal tree size under the 1-SE rule reported in the 10-fold cross-validation analysis (Fig. 3 (a)). The first split in the tree was based on the distance from the nearest beach access point, with values $< = 144$ m indicating that oystercatchers were predominantly absent (n = 45). When distance from access point was > 144 m, the next split was decided by the ranking of beach disturbance. Oystercatchers were predominantly absent from highly disturbed beaches (RANK = 3, n = 14). On less disturbed beaches (RANK = 0, 1, 2) the habitat suitability index was the next splitting variable, with most occurrence records in less suitable habitat (HABITAT $< = 0.57$, n = 41). The first three branches of the classification tree explain most of the variation in the tree, as indicated by the length of the branches.

The regression tree model did not perform quite as well, explaining only 37% of the total variation in the tree with a cross-validation error rate of 0.65 (Fig. 2). We chose a final tree with only three terminal nodes, which was smaller then the modal tree size indicated by the cross-validation plot (Fig. 3 (b)) because the more parsimonious tree was within 1-SE of the minimum error tree and the total error rate was high for all trees. The results of the final model showed strong relationships between oystercatcher abundance and two explanatory variables: habitat suitability and beach rank. When the habitat suitability index was > 0.71, the mean density of oystercatchers was 4.50 / 100 m (n = 8). When the index was $< = 0.71$, the remaining training data were split by beach rank, with highly disturbed beaches reporting a much lower density (0.11 / 100 m, n = 57) than less disturbed beaches (1.07 / 100 m, n = 71).

Variable importance in the CART models was based on the total variation explained by each variable at all nodes in the tree (Table 2). The three most important variables in the classification tree model were the same as those indicated by the final tree presented in Fig. 1. In the regression tree model, distance from access point contributed substantially to the final model although it was excluded from the three-node tree presented in Fig. 2. The explanatory variable for driving on beaches in May did not show up in either of the final CART models; however, this variable did contribute to each of the final models. Driving in other months contributed to a lesser degree.

Random Forests Model

The random forests model also performed well, exhibiting good discrimination ability (AUC = 0.94). Further, the total misclassification rate for the model was low at 10.30%. Contrary to expectations, however, this modeling technique did not perform much better than the simple classification tree model (AUC = 0.93). The top four explanatory variables contributing to the final random forests model were the same as those for the classification tree model; however, the ranking of variable importance was ordered differently (Table 2). The most noticeable difference was that distance from access point dropped to the second most important variable while beach rank became the most important variable. This was likely due to the classification tree model allowing surrogate values to be used for missing data while the random forests did not, and there were missing values in the beach access variable that used beach rank as the surrogate

values. Another difference between the random forests and CART models was that habitat suitability became less important than driving on beaches in May, which became the third most important explanatory variable on oystercatcher distribution.

MAXENT Model

The MAXENT model performed better than either of the two previous models, exhibiting very good discrimination ability (AUC = 0.98). The variable contributions to the MAXENT model were ranked in the same order as those for the random forests model (Table 2). One difference between the MAXENT model and the other models was the relative contribution of the variables for driving in months other than May. In the MAXENT model, these explanatory variables have little or no contribution to the final model.

In order to illustrate the effects that the most important explanatory variables had on the MAXENT distribution we included response curves for the top four contributing variables (Fig. 4). The response curves offer additional insight into the intensity and direction of the response. The response curves show that there was a very low probability of oystercatcher presence on highly disturbed beaches (RANK = 3). Additionally, oystercatchers were not predicted to occur on beaches that permit driving in May (DRIVE05 = 1). Finally, the probability of oystercatcher presence increased substantially as the distance from access points and habitat suitability values increased.

DISCUSSION

In conservation based studies it is inevitable that a species will not occupy all suitable habitat (Fielding & Bell 1997). Metapopulation theory and source-sink dynamics predict that a species will occupy a broad range of habitat suitability (Akcakaya et al. 2003; Pulliam 1988). Thus, only a small percentage of highly suitable habitat will be occupied at any given time and the actual distribution may be quite different than the predicted realized niche of the species (Pulliam 2000). In unsaturated populations, available highly suitable habitat should be filled if the population expands (Fielding & Bell 1997). The amount of highly suitable oystercatcher habitat along the New Jersey coastline is severely limited; however, there are areas on the state's barrier beaches predicted to be highly suitable that lack oystercatchers altogether or that have very low densities of breeding pairs. Our results suggest that human disturbance is causing oystercatchers to avoid these highly suitable areas.

All of the modeling techniques used in this study showed good discrimination ability based on AUC values. The MAXENT model (AUC = 0.98) outperformed both the classification tree model (AUC = 0.93) and random forests model (AUC = 0.94); however, all models were useful in predicting the distribution. The classification tree model proved very effective with similar results as the more complex techniques, and provided results that were easy to interpret, making this a useful technique.

The top four explanatory variables contributing to the distribution were identical for all classification techniques, although the rank order was different. In the absence of human disturbance, there should be a high probability of oystercatcher presence on barrier beaches with high habitat suitability values. However, habitat suitability contributes much less to the overall distribution than expected in all models, indicating that other factors affect the distribution to a greater degree. The top two variables in all models were distance from nearest beach access point and beach rank indicating that recreational disturbance trumps habitat suitability in predicting the local oystercatcher distribution. The regression tree model provides evidence that oystercatchers are most abundant in highly suitable habitat (density = 4.50 pairs / 100 m), and that oystercatchers are least abundant in less suitable habitat when combined with high levels of recreational disturbance (density = 0.11 pairs / 100 m). Thus, oystercatchers are crowding into the small areas of highly suitable breeding habitat that are protected from human disturbance.

As expected, there is a temporal effect of driving on beaches on oystercatcher distribution. Driving in the month of May, which is the peak nest initiation period for oystercatchers in New Jersey (T. Virzi, personal observation), influences the distribution to some degree in all of the models. In the MAXENT and random forests models, this explanatory variable surpasses habitat suitability in importance. We interpret this as evidence that driving on beaches in May is displacing oystercatchers from habitat that might otherwise be used for nesting.

American Oystercatchers appear to be moving into saltmarsh habitat in greater numbers in New Jersey in response to the high levels of human disturbance on barrier beaches. Non-traditional, river island nesting habitat used by American Oystercatchers breeding in North Carolina were considered sub-optimal and were thought to be functioning as ecological traps (McGowan et al. 2005). If American Oystercatchers in New Jersey are moving into saltmarsh habitat due to lower levels of human disturbance there but are experiencing lower reproductive success in this habitat for other reasons, the marshes may be acting as ecological traps as well.

Although the results of our nest success study in Chapter 1 did not indicate that human disturbance was among the most important factors affecting oystercatcher nest success, other studies have shown that disturbance alters oystercatcher incubation behavior (McGowan 2006; Sabine 2006; Sabine 2008) and chick rearing ability (Leseberg 2000). Thus, reproductive output could be directly reduced in response to high levels of disturbance. Human disturbance could also indirectly affect reproductive output if density-dependent factors alter breeding behavior. The severe reduction of highly suitable breeding habitat on barrier beaches may force oystercatchers to breed in higher than normal densities in the limited remaining suitable habitat, which is a hypothesis supported by the differential densities shown in our regression models. Reproductive success for oystercatchers may be reduced in several ways if all breeding individuals continue to be crowded into smaller and smaller areas. Clutch size and reproductive output are reduced in many oystercatcher species at high breeding densities (Hockey 1996). Further, competition for nest-sites could lead to decreased fitness for some

individuals if they are forced to breed in sub-optimal habitat or are excluded from breeding altogether (Ens 1992).

The species distribution modeling techniques we implemented are useful tools for conservation biologists. We have shown that CART models are easy to use and interpret, making them ideal for analyzing the effects of explanatory variables on species distributions. The results of our CART models show that both recreational disturbance and driving on beaches affect the distribution of oystercatchers, providing conservation managers with valuable information that should help them make informed decisions as to where and when restrictions on beach access or driving should be implemented.

We recommend that beach access be restricted during the months of April through July in any areas that have highly suitable habitat (as predicted by the habitat suitability model in Chapter 2), especially when those areas are distant from public access points (> 144 m). These areas are severely limited in New Jersey since most barrier beaches are already highly developed. Therefore, the few beaches where these conditions exist are high priority areas for protection. Further, we recommend that all beaches be closed to driving no later than May 1 to encourage settlement by breeding oystercatchers, and potentially other threatened and endangered beach-nesting birds. Future studies should examine the effects of different types of recreational disturbance on oystercatcher distribution and reproductive performance, especially in alternative breeding habitats such as saltmarsh, inlet and dredge-spoil islands where oystercatchers are predicted to be most prevalent.

Further, research into appropriate buffer distances to minimize the effects of recreational disturbance should also be conducted.

ACKNOWLEDGEMENTS

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TABLES

Table 1: Description of explanatory variables used in species distribution models for American
oystercatcher distribution in coastal New Jersey in 2007.

Variable	Description	Data Type	Predicted Association	Data Range
HABITAT	Habitat suitability index (probability of oystercatcher presence) based on previous species distribution model (Chapter 2)	Continuous	Higher = More Abundant	0.00 - 0.82 (Low - High)
RANK	Ranking of beaches by approximate level of recreational disturbance; based on ownership/management of land, extent of coastal development, and personal observations (T. Virzi)	Categorical	Higher = Less Abundant	0 - Very Low 1 - Low 2 - Moderate 3 - High
DRIVE06	Driving on beach allowed during June	Categorical	Driving = Not Present	0 - No 1 - Yes
DRIVE05	Driving on beach allowed during May	Categorical	Driving =	0 - No

			Not Present	1 - Yes
DRIVE04	Driving on beach allowed during April	Categorical	Driving =	0 - No
			Not Present	1 - Yes
DRIVE03	Driving on beach allowed during March	Categorical	Driving =	0 - No
			Not Present	1 - Yes

[a]Variable was excluded from training data for all data points on beaches where public access was completely restricted. For the Maxent model, a value of -9999 was used to indicate the missing data.

[b]Predicted association with oystercatcher probability of presence or abundance.

Table 2. Variable contributions to species distribution models for American oystercatcher

distribution in New Jersey in 2007. Numbers in parentheses indicate rank of variable importance

in the final model.

Variable	Classification Tree		Regression Tree		Random Forests		Maxent Model	
ACCESS	40.9	(1)	17.5	(3)	27.4	(2)	27.5	(2)
RANK	28.9	(2)	18.2	(2)	44.4	(1)	56.6	(1)
HABITAT	12.0	(3)	55.5	(1)	9.6	(4)	7.0	(4)
DRIVE05	9.9	(4)	6.1	(4)	10.6	(3)	8.8	(3)
DRIVE03	6.4	(5)	0.0		1.6	(7)	0.0	
DRIVE06	1.4	(6)	0.0		4.2	(5)	0.1	(5)
DRIVE04	0.3	(7)	2.8	(5)	2.4	(6)	0.0	
	100.0		100.0		100.0		100.0	

FIGURE LEGENDS

Fig. 1. Classification tree analysis showing probability of oystercatcher presence or absence in response to human disturbance in coastal New Jersey in 2007. Splitting variables and their decision values are recorded at each non-terminal node of the tree. The length of each branch is proportional to the variation explained by the variable used at each split. Each terminal node is labeled (classified) according to whether oystercatchers are predominantly present or absent, and includes the proportion and number (in parentheses) of observations in that class. The misclassification rates for training and test data were 9.6% and 15.4%, respectively.

Fig. 2. Regression tree analysis showing the effect of human disturbance on oystercatcher abundance in coastal New Jersey in 2007. Splitting variables and their decision values are recorded at each non-terminal node of the tree. Each terminal node is labeled with the mean number of oystercatcher pairs occurring within a 100 m radius surrounding each training data point, SD, and the number of observations at the node (in parentheses). The length of each branch is proportional to the variation explained by the variable used for each split. The tree explained 37.1% of the total sum of squares.

Fig. 3. Cross-validation plots for (a) the classification tree analysis and (b) the regression tree analysis. Plots report the relative error for a single representative 10-fold cross-validation and include 1-SE estimates for each tree size used in the analyses. The dashed lines indicate the 1-SE cutoff above the minimum error values for each analysis. The bar charts show the relative proportions of trees of each size used in each analysis based on the 1-SE rule (white bars) and minimum error rule (black bars) from a series of 50 cross-validations. The most likely tree size in each analysis (7 nodes) was determined by the modal size (under the 1-SE rule) reported in each series of cross-validations. We chose to use a more parsimonious tree (3 nodes) for our regression analysis since this sized tree was within the 1-SE rule, and since the total relative error rate did not improve much by using the larger tree.

Fig. 4. Variable response curves based on the final Maxent model for the four most important explanatory variables for American oystercatcher species distribution models in coastal New Jersey in 2007. The response curves show the effects of the top four variables on the predicted probability of oystercatcher presence taking into consideration dependencies induced by correlations between variables. The first explanatory variable (RANK) is a categorical variable for the level of human disturbance, with the following parameter values: 0 – very low, 1 – low, 2 – moderate, and 3 – high. The second variable (DRIVE05) is also categorical with values of 0 (beach closed to driving during May) or 1 (beach open to driving during May). The third variable (ACCESS) is a continuous variable for the distance to nearest access point in meters. The final variable (HABITAT)

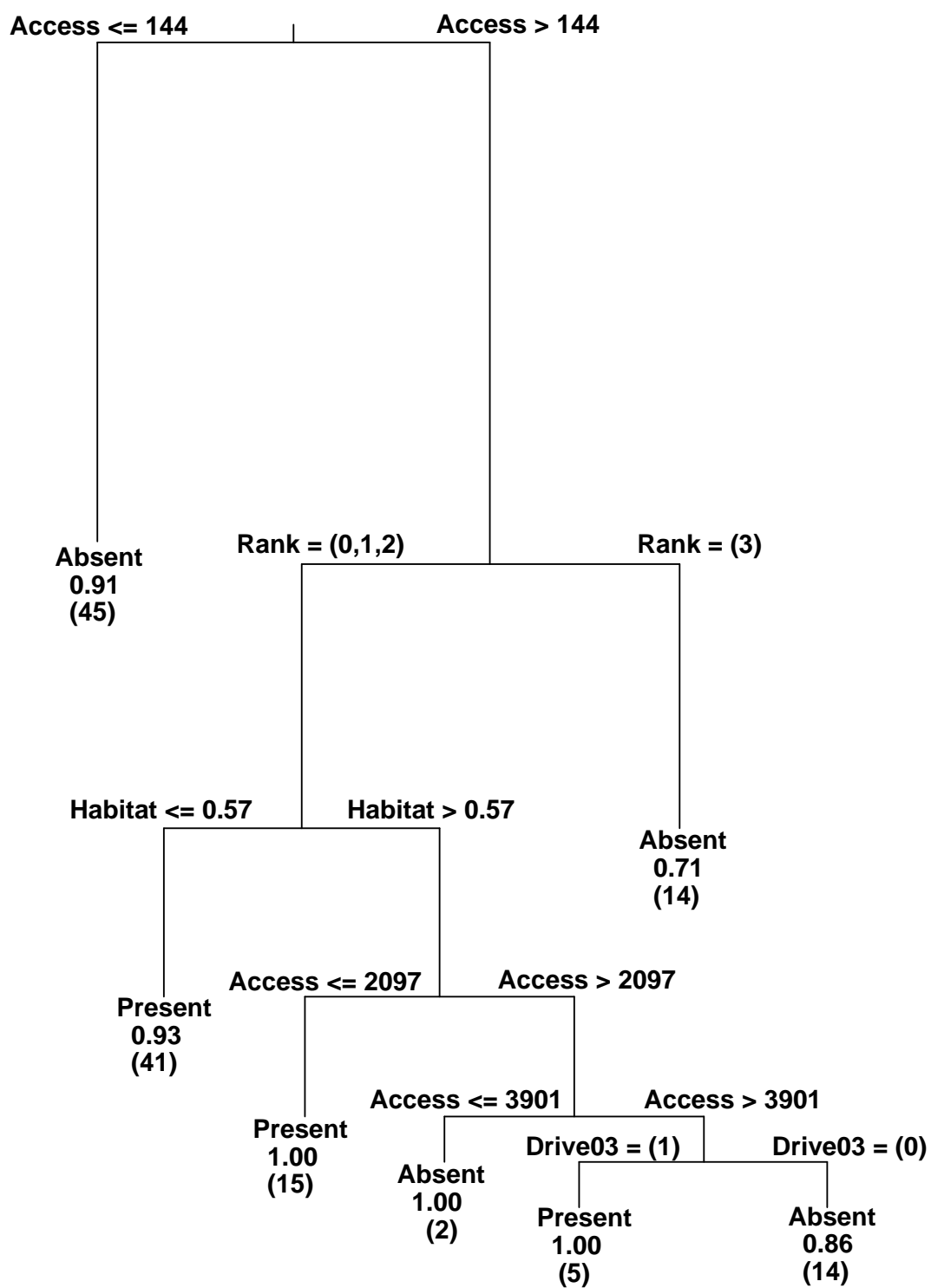is a continuous variable for based on habitat suitability values, with higher values indicating higher suitability.
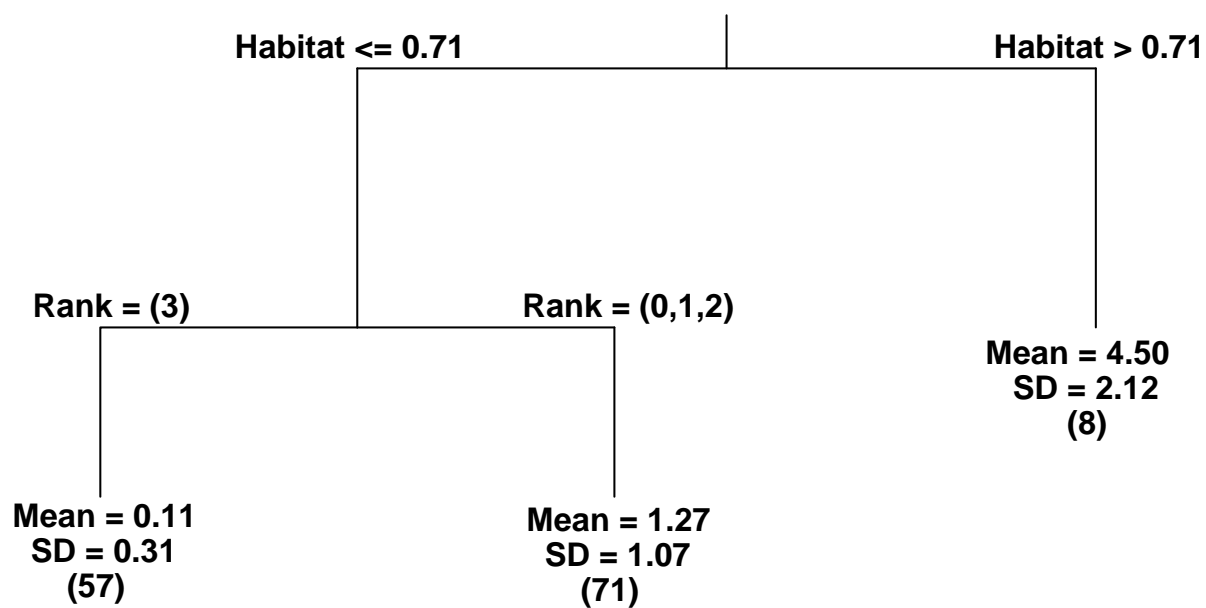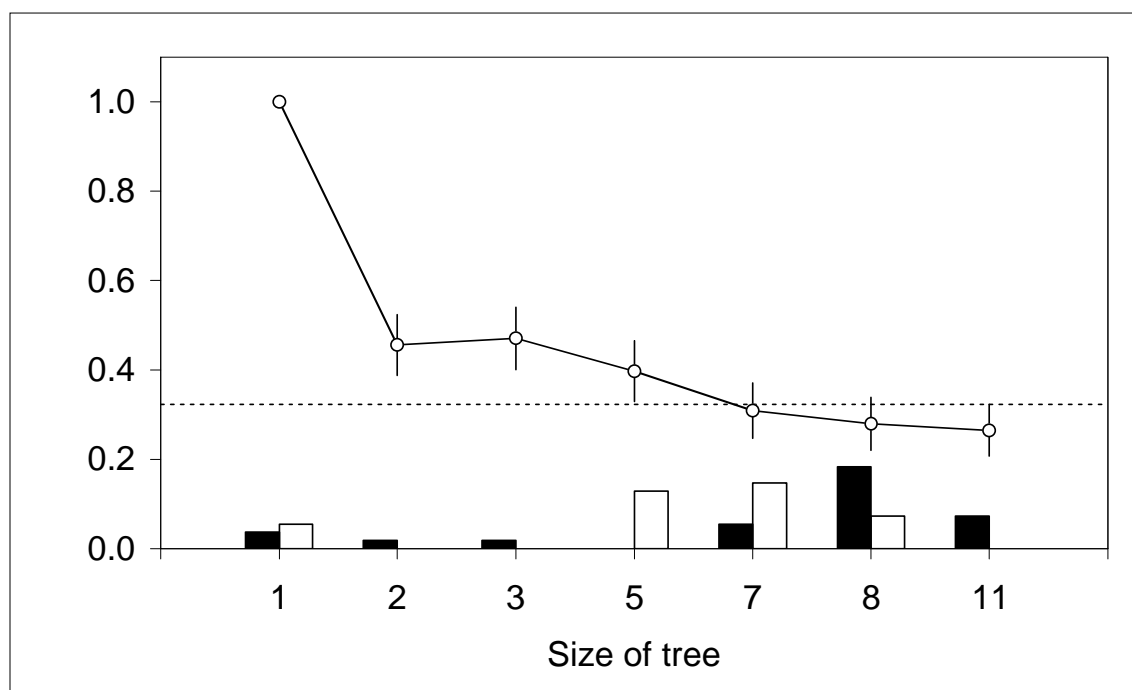
FIGURES

Fig. 1

Fig. 2

Fig. 3 (a)

Fig. 3 (b)

Fig. 4

RANK   DRIVE05

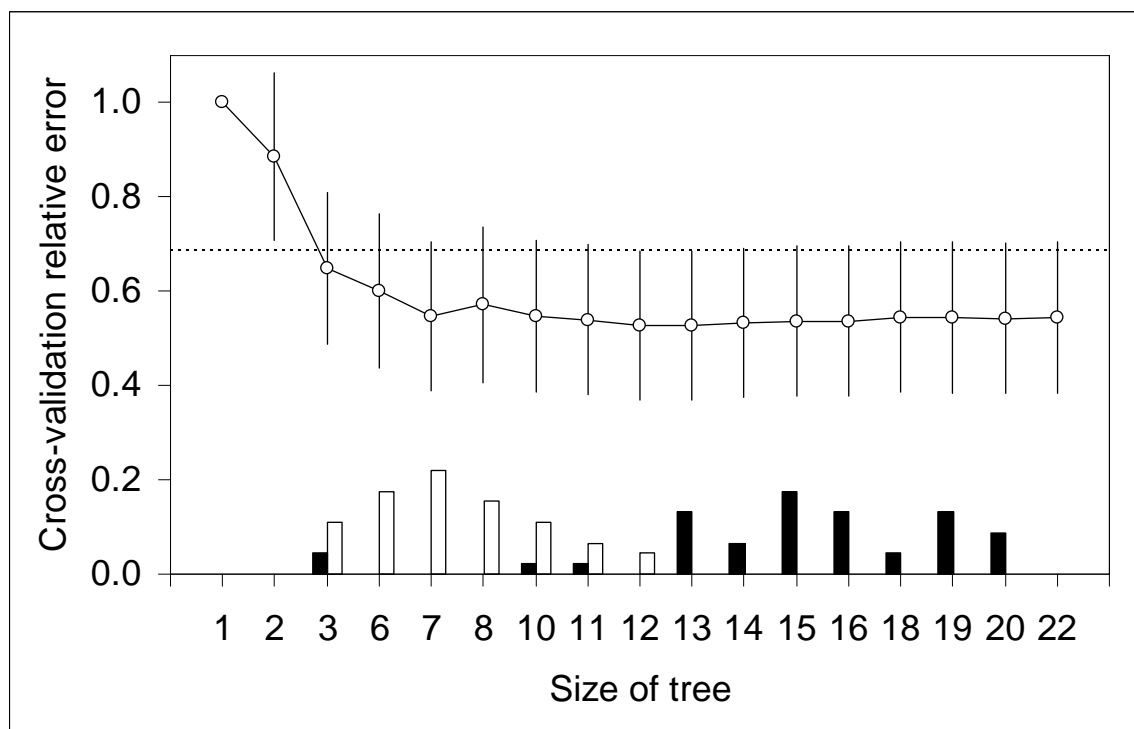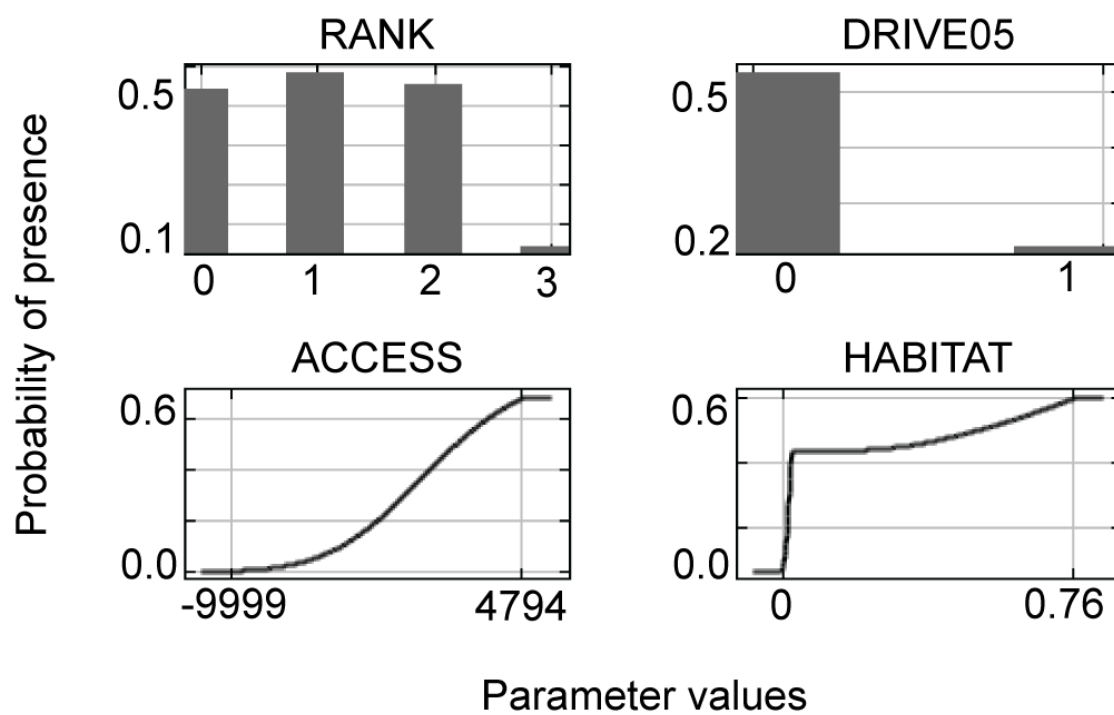ACCESS   HABITAT

Probability of presence

Parameter values

CONCLUDING REMARKS

The overarching question of my initial research was, "How does human disturbance on breeding grounds affect the reproductive performance of American oystercatchers?" I began by exploring the direct effects of human disturbance on oystercatcher nest success, hypothesizing that high levels of human disturbance would limit overall reproductive performance. However, during the course of my research I realized that the direct effects of human disturbance were likely less important than the indirect effects. My dissertation shifted directions towards attempting to understand the effects of coastal development and human disturbance on the distribution of American oystercatchers in the highly urbanized coastal ecosystems of New Jersey.

At the outset of my study, little was known about the distributional patterns of oystercatchers in non-traditional (alternative) habitats such as saltmarsh, inlet, back-bay and dredge-spoil islands. Oystercatchers were known to utilize these alternative habitats to breed, but little was known about the extent of occurrence in these habitats, nor about reproductive rates in these habitats. Further, the distribution and overall population size of American oystercatchers in New Jersey was poorly understood. Through my research, I was able to answer some of these questions adding significantly to the body of knowledge about American oystercatcher distribution, breeding habitat requirements and reproductive rates.

In CHAPTER 1, I analyzed various human-induced effects on oystercatcher daily nest survival rates and overall reproductive performance across a mosaic of habitats. I used an information theoretic approach to analyze the effects, which to my knowledge had not been done previously for the American oystercatcher. My results showed that the principal factor negatively influencing daily survival rates of both clutches and broods was the presence of mammalian predators. Further, the presence of mammalian predators was much more important in predicting the daily survival rate of nests than human disturbance, which proved not to be an important contributing factor at all.

The daily survival rates were used to derive nest success rates for oystercatchers, and these rates were compared between habitat types. The strong effect of the presence of mammalian predators, primarily red foxes (*Vulpes vulpes*) (T. Virzi, personal observation), can be seen by comparing nest success rates between habitats. The nest success rate on predator-free islands (21%) was an order of magnitude greater than the rate reported on barrier islands (2%), which have high densities of predatory mammals. The nest success rate in saltmarsh habitat (11%) was also substantially lower than the rate reported in the most productive habitat, likely due to flooding of these low lying nests during regular spring tides. The overall nest success rate for American oystercatchers breeding in New Jersey is alarmingly low (4%), thus the state's population is unlikely to be able to sustain itself at the current reproductive rates.

In CHAPTER 2, I analyzed the factors influencing the local distribution of breeding oystercatchers in New Jersey. This was the first such attempt for the local population,

and to my knowledge for American oystercatchers anywhere in their range. I used a novel presence-only species distribution modeling technique (MAXENT) to derive a predictive model of oystercatcher distribution on barrier beaches and in alternative habitats along the entire New Jersey coastline. The model was based on a suite of environmental variables that I considered important to breeding oystercatchers, but also included explanatory variables for the extent of urbanization. The predictive model was then validated by independent ground surveys conducted in areas that were previously unsurveyed in an attempt to locate new oystercatcher populations. I hypothesized that oystercatchers were using alternative habitats to breed in very high densities, and that the New Jersey oystercatcher population was likely much larger than thought.

The MAXENT model performed very well, proving to be effective at predicting the realized niche of the species. At a regional scale, the model predictions were useful to locate new oystercatcher populations. However, at a local scale the predictions were not validated by the actual distribution. I attributed this to source-sink dynamics affecting the actual distribution due to a severe limitation of highly suitable breeding habitat along the New Jersey coast. Still, the models did provide predictions that helped me to locate areas where a significant number of oystercatchers were breeding in alternative habitat. Overall, 309 breeding pairs of American oystercatchers were located during the course of my surveys. This vastly improved the estimate of the state's breeding population, which was previously thought to be approximately 60 pairs. Most oystercatchers (69%) were found in saltmarsh habitat, with fewer pairs (19%) found on barrier beaches and the remainder (12%) found on natural or artificial islands, supporting my hypothesis that

oystercatchers were utilizing alternate breeding habitat to a larger degree than previously suspected.

The vast majority of New Jersey oystercatchers breed in habitat where reproductive rates are very low (barrier beaches and saltmarshes). Further, most oystercatchers breed in saltmarsh habitat, which may be acting as sink habitat for the population. Additional research is necessary to understand if saltmarsh habitat is indeed acting as sink habitat. Examining local movement patterns between habitats and across years would help us to understand if oystercatchers are using saltmarsh temporarily while waiting for better habitat to become available, or if they are choosing saltmarsh habitat as their preferred habitat. In the latter case, saltmarshes may be acting as ecological traps for the species.

In CHAPTER 3, I examined the indirect effect of human disturbance on the reproductive performance of American oystercatchers by modeling the species' distribution in response to recreational activity on barrier beaches. I used classification and regression tree (CART) models to identify the principal factors influencing local oystercatcher distributional patterns. Using CART models, I was able to build upon the habitat suitability model conducted in Chapter 2 by adding explanatory variables for human disturbance. I hypothesized that persistent human disturbance on barrier beaches displaced oystercatchers from the most highly suitable breeding habitat.

The CART models indicated that human disturbance is indeed affecting the local distributional patterns of American oystercatchers on barrier beaches in New Jersey. The

probability of oystercatcher presence was lower on highly disturbed beaches and in areas that are in close proximity to beach access points. Further, driving on beaches during the month of May negatively affected the distribution, with oystercatchers possibly being completely displaced from these beaches regardless of habitat suitability.

My research has shown that coastal development and human disturbance may not be directly affecting American oystercatcher reproductive performance, but that indirect effects due to changes in local distributional patterns may contribute to lower productivity. Oystercatchers in New Jersey are being displaced from highly suitable breeding habitat due to high levels of human disturbance, especially on barrier beaches, and individuals are crowding into the limited remaining suitable breeding habitat. The long-term population consequences of this distributional pattern could be severe. In some areas (saltmarshes) it is possible that high use of alternative habitat could be acting as an ecological trap for the species. In other areas (inlet or dredge-spoil islands) productivity can be very high; however, if individuals continue to be crowded into these limited areas there could be other density-dependent factors that might further reduce reproductive rates. On barrier beaches, it may seem like a good thing that oystercatchers are being displaced from this habitat, which has shown poor reproductive rates. However, with proper management of mammalian predators this preferred habitat of the American oystercatcher could become productive for the species.

The most beneficial management option for the species would be to increase the amount of suitable breeding habitat available for oystercatchers. Providing some protection from

human disturbance on barrier beaches could encourage settlement, and thus reduce the number of oystercatchers breeding in saltmarsh habitat. However, predation pressure on barrier beaches may still be very high without intensive predator control management. Still, providing more choices for oystercatchers may spread out predation risk across larger spatial scales. The protection of highly suitable alternative breeding habitat (isolated islands) would also be an effective management strategy given the differential nest success rates that I have shown here. Further, additional habitat in the form of dredge-spoil islands could be created. The ultimate goal should be to provide enough suitable habitats so that American oystercatchers have choices rather than forcing the entire population to rely on smaller and more fragmented areas for breeding.

Curriculum Vitae

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Education

Institution	Degree	Year
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Rutgers University	Ph.D. – Ecology & Evolution	2008

Employment

2008
Rutgers University, New Brunswick, NJ
Part-Time Lecturer of Wildlife Ecology and Conservation

2006 – 2008
Rutgers University, New Brunswick, NJ
Part-Time Lecturer of Ornithology

2005 – 2007
Rutgers University, New Brunswick, NJ
Teaching Assistant – Field Techniques in Ecology & Natural Resources

2005
Rutgers University**,** New Brunswick, NJ
Teaching Assistant – Ornithology

2004 – 2005
Rutgers University**,** New Brunswick, NJ
Graduate Student Research Associate

2003 – 2004
New Jersey Division of Fish and Wildlife, Trenton, NJ
Environmental Educator – Sedge Island Natural Resource Education Center

1997 – 2008
Virzi Consulting**,** Manasquan, NJ
Accredited Business Valuation Analyst

1987 – 1997
Various Public Accounting Firms
Certified Public Accountant