The effect of human disturbance on the local distribution of American Oystercatchers breeding on barrier island beaches

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On the barrier beaches of New Jersey, USA, 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 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. I 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. My 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, I 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.

INTRODUCTION

American Oystercatchers *Haematopus 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 on the east coast of North America 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. 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. Here, I 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 (Virzi *et al.* 2008).

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 recent 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). I used CART models to identify the most important variables explaining the distribution of American Oystercatchers in response to recreational activity.

A number of other species distributional modeling techniques have been used in recent decades including 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). These models may also be used to predict the realized niche at a smaller scale by including finer-scale predictor variables (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 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, I develop and compare simple CART models with other more complex species distribution modeling techniques. Virzi *et al.* (2008) modeled the realized niche of the American Oystercatcher in New Jersey based on environmental variables and the extent of urbanization. The 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 Virzi *et al.* (2008) 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 (Davis *et al.* 2001), highly suitable habitat that is unsaturated should be filled first before any shift into alternative habitat (Fielding & Bell 1997). I 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 my 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

I used presence and absence records as training data for my species distribution models. These data were provided by ground surveys conducted during 2007 along all Atlantic Ocean-facing beaches in New Jersey (see Virzi *et al.* 2008 for methods). The surveys identified 68 occurrence records (i.e. breeding pairs) that I used as presence data in my models. I also included 68 absence records in my models; absence was confirmed during the surveys based on visits to randomly selected points within the study areas. For all occurrence records the total number of breeding pairs located within a 100 m radius was provided, and this was used for analysis of abundance in my regression tree models.

Explanatory variables

My distribution modeling techniques required the creation of a set of explanatory variables that were used as background data over which the distribution of presence and absence records were modeled (Table 1). Virzi *et al.* (2008) 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. I 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 my species distribution models was the habitat suitability index provided by Virzi *et al.* (2008), 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), I selected an *a priori* set of explanatory variables that I hypothesized would influence oystercatcher distribution at a local scale. Thus, I chose six additional explanatory variables related to recreational disturbance on barrier beaches (Table 1). I 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).

I 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. I 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

I 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 my 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, I 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. 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).

I used CART software version 6.0 (Salford Systems, San Diego, CA, USA) for all CART analyses. In all models, I used the Gini index for measuring the homogeneity of nodes, a 10-fold cross-validation process, and allowed surrogate values for missing explanatory variables. I determined the final tree size in each analysis by examining a series of 50 cross-validations so that I 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, I 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.

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

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 (Virzi *et al.* 2010)	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 = Not Present	0 – No 1 – Yes
Drive04	Driving on beach allowed during April	Categorical	Driving = Not Present	0 – No 1 – Yes
Drive03	Driving on beach allowed during March	Categorical	Driving = Not Present	0 – No 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.

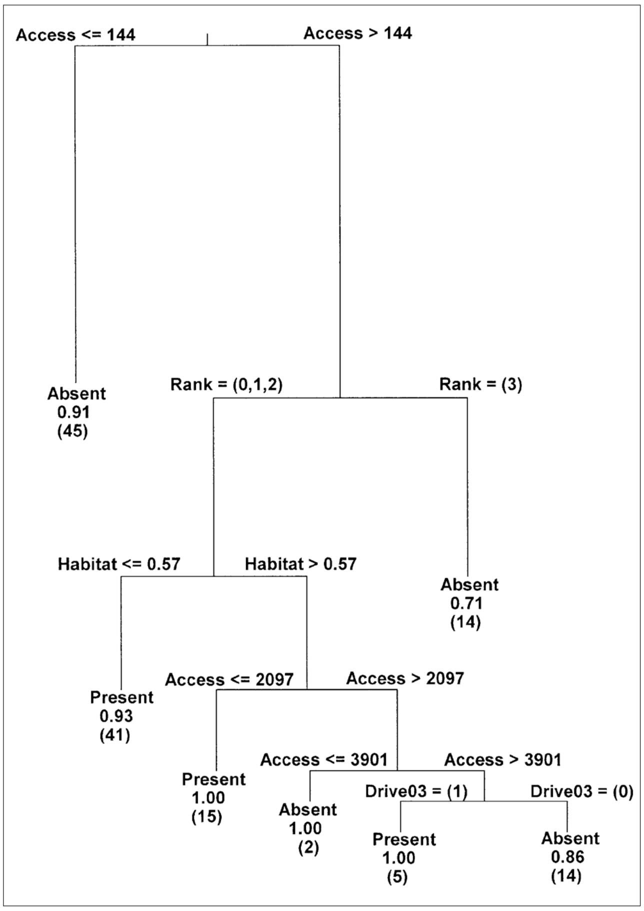

Fig. 1. Classification tree analysis showing probability of oystercatcher presence or absence in response to human disturbance in coastal New Jersey in 2007. Splitting variables and their decision values are recorded at each non-terminal node of the tree. The length of each branch is proportional to 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.

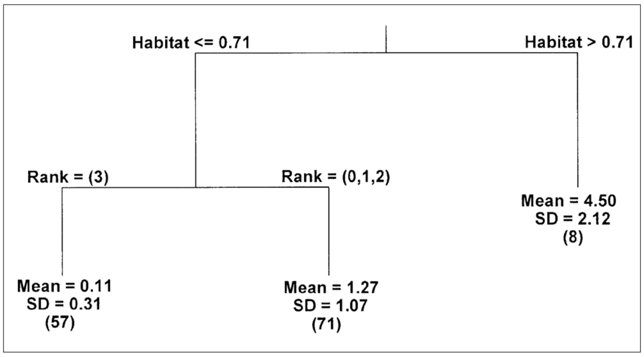

Fig. 2. Regression tree analysis showing the effect of human disturbance on oystercatcher abundance in coastal New Jersey in 2007. Splitting variables and their decision values are recorded at each non-terminal node of the tree. Each terminal node is labeled with the mean number of oystercatcher pairs 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.

Finally, I used a species distribution modeling approach developed in a machine-learning environment (MAXENT) (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).

I used MAXENT software version 3.2.1 (which is freely available for download from *http://www.cs.princeton.edu/~schapire/maxent*) to run maximum entropy models. I ran my 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, I 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 to 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).

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. 3a). 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). I chose a final tree with only three terminal nodes, which was smaller than the modal tree size indicated by the cross-validation plot (Fig. 3b) because the more parsimonious tree was within 1-SE of the

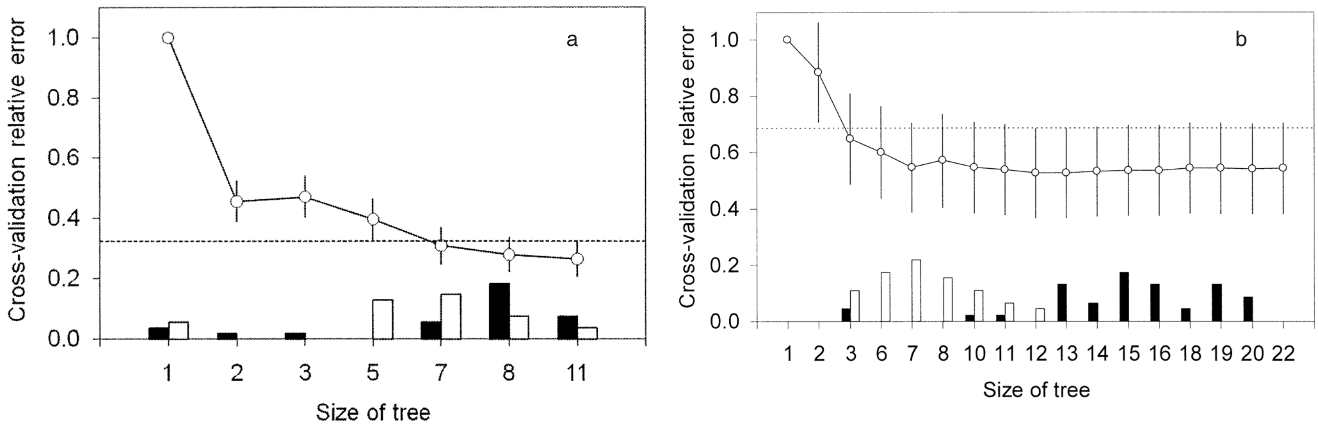

Fig. 3. Cross-validation plots for (a) the classification tree analysis and (b) the regression tree analysis. Plots report the relative error for a single representative 10-fold cross-validation and include 1-SE estimates for each tree size used in the analyses. The dashed lines indicate the 1-SE cutoff 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.

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 per 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 per 100 m, n = 57) than less disturbed beaches (1.07 per 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%. However, this modeling technique did not perform much better than the simpler 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

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	

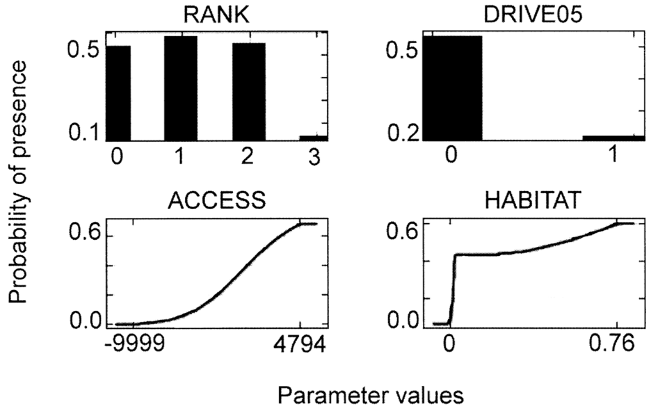

Fig. 4. Variable response curves based on the final Maxent model for the four most important explanatory variables for American Oystercatcher species distribution models in coastal New Jersey in 2007. The response curves show the effects of the top four variables on the predicted probability of oystercatcher 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.

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 I 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, showing 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. My 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 per 100 m), and that oystercatchers are least abundant in less suitable habitat when combined with high levels of recreational disturbance (density = 0.11 pairs per 100 m). Thus, oystercatchers are crowding into the small areas of highly suitable breeding habitat that are protected from human disturbance.

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, pers. obs.), 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. I 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 habitats 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.

Virzi *et al.* (2010) found that human disturbance was not among the most important factors affecting oystercatcher nest success; however, other studies have shown that disturbance alters oystercatcher incubation behavior (McGowan 2006, Sabine 2006, 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 my 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 (e.g. intraspecific competition for food resources on high density islands may reduce chick survival and fledge rates for some individuals). 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 current distribution of oystercatchers in New Jersey may be limiting the population growth rate due to the number of individuals crowding into sub-optimal marsh habitat. Even though the local population growth rate may be a limiting factor, the population size in New Jersey is likely to remain relatively stable looking forward due to immigration from other parts of the species' range as the species continues a northward range expansion. However, the proportion of individuals currently using sub-optimal habitat is likely to remain unchanged unless more highly suitable beach habitat becomes available. Unless additional highly suitable breeding habitat becomes available for oystercatchers in New Jersey it is possible that this population could act as a sink for the overall oystercatcher population. Creation of additional barrier beach habitat in New Jersey is highly unlikely since most of the coastal land there is already heavily developed. The best way to create more highly suitable breeding habitat is to improve conditions on existing undeveloped sections of beaches.

One way to improve conditions on existing beaches would be to restrict access during the months of April through July in any areas that have highly suitable habitat, 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, all beaches predicted to be highly suitable habitat should 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.

The species distribution modeling techniques I implemented are useful tools for conservation biologists. I 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 my 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.

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REFERENCES

Agness, A.M., J.F. Piatt, J.C. Ha & G.R. VanBlaricom. 2008. Effects of vessel activity on the near-shore ecology of Kittlitz's murrelets (*Brachyramphus brevirostris*) in Glacier Bay, Alaska. *Auk* 125: 346–353.

Akcakaya, H.R., J.L. Atwood, D. Breininger, C.T. Collins & B. Duncan. 2003. Metapopulation dynamics of the California least tern. *J. Wildlife Man.* 67: 829–842.

Berk, R.A. 2006. An introduction to ensemble methods for data analysis. *Sociol. Methods & Res.* 34: 263–295.

Bourg, N.A., W.J. McShea & D.E. Gill. 2005. Putting a cart before the search: Successful habitat prediction for a rare forest herb. *Ecology* 86: 2793–2804.

Breiman, L., J.H. Friedman, R.A. Olshen & C.J. Stone 1998. *Classification and regression trees.* Chapman & Hall, New York, NY.

Brown, S.C., S. Schulte, B. Harrington, B. Winn & M. Howe. 2005. Population size and winter distribution of eastern American Oystercatchers. *J. Wildlife Man.* 69: 1538–1545.

Burger, J. 1991. Foraging behaviour and the effects of human disturbance on the piping plover *Charadrius melodus*. *J. Coastal Res.* 7: 39.

Burnham, K.P. & D.R. Anderson. 2002. *Model selection and multi-model inference: a practical information–theoretic approach.* Springer-Verlag, New York, NY.

Cardoni, D.A., M. Favero & J.P. Isacch. 2008. Recreational activities affecting the habitat use by birds in Pampa's wetlands, Argentina: Implications for waterbird conservation. *Biol. Conserv.* 141: 797–806.

Carney, K.M. & W.J. Sydeman. 1999. A review of human disturbance effects on nesting colonial waterbirds. *Waterbirds* 22: 68–79.

Colwell, M.A., C.B. Millett, J.J. Meyer, J.N. Hall, S.J. Hurley, S.E. McAllister, A.N. Transou & R.R. LeValley. 2005. Snowy Plover reproductive success in beach and river habitats. *J. Field Ornith.* 76: 373–382.

Cutler, D.R., T.C. Edwards, K.H. Beard, A. Cutler & K.T. Hess. 2007. Random forests for classification in ecology. *Ecology* 88: 2783–2792.

Davis, M.B., T.R. Simons, M.J. Groom, J.L. Weaver & J.R. Cordes. 2001. The breeding status of the American Oystercatcher on the east coast of North America and breeding success in North Carolina. *Waterbirds* 24: 195–202.

De'Ath, G. 2007. Boosted trees for ecological modeling and prediction. *Ecology* 88: 243–251.

De'Ath, G. & K.E. Fabricius. 2000. Classification and regression trees: a powerful yet simple technique for ecological data analysis. *Ecology* 81: 3178–3192.

Dudik, M., S.J. Phillips & R.E. Schapire. 2007. Maximum entropy density estimation with generalized regularization and an application to species distribution modeling. *J. Machine Learning Res.* 8: 1217–1260.

Elith, J., C.H. Graham, R.P. Anderson, M. Dudik, S. Ferrier, A. Guisan, R.J. Hijmans, F. Huettmann, J.R. Leathwick, A. Lehmann, J. Li, L.G. Lohmann, B.A. Loiselle, G. Manion, C. Moritz, M. Nakamura, Y. Nakazawa, J.M. Overton, A.T. Peterson, S.J. Phillips, K. Richardson, R. Seachetti-Periera, R.E. Schapire, J. Soberon, S. Williams, M.S. Wisz & N.E. Zimmerman. 2006. Novel methods improve prediction of species' distributions from occurrence data. *Ecography* 29: 129–151.

Ens, B.J. 1992. The despotic distribution and deferred maturity in the oystercatcher: two sides of the same coin. pp. 81–109. *The Social Prisoner: Causes of Natural Variation in Reproductive Success of the Oystercatcher*. Van Denderen B.V., Groningen.

Erwin, M.R. 1980. Breeding habitat use by colonially nesting waterbirds in two mid-Atlantic U.S. regions under different regimes of human disturbance. *Biol. Conserv.* 18: 39–51.

Fielding, A.H. & J.F. Bell. 1997. A review of methods for the assessment of prediction errors in conservation presence/absence models. *Envir. Conserv.* 24: 38–49.

Flemming, S.P., R.D. Chiasson, P.C. Smith, P.J. Austin-Smith & R.P. Bancroft. 1988. Piping Plover status in Nova Scotia related to its reproductive and behavioral response to human disturbance. *J. Field Ornith.* 59: 321–330.

Gibson, L., B. Barrett & A. Burbidge. 2007. Dealing with uncertain absences in habitat modelling: a case study of a rare ground-dwelling parrot. *Divers. & Distrib.* 13: 704–713**.**

Gill, J.A., W.J. Sutherland & A.R. Watkinson. 1996. A method to quantify the effects of human disturbance on animal populations. *J. App. Ecol.* 33: 786–792.

Guisan, A., T.C.J. Edwards & T. Hastie. 2002. Generalized linear and generalized additive models in studies of species distributions: setting the scene. *Ecol. Modelling* 157: 89–100.

Hockey, P.A.R. 1987. The influence of coastal utilization by man on the presumed extinction of the Canarian Black Oystercatcher *Haematopus meadewaldoi. Biol. Conserv.* 39: 49–62.

Hockey, P.A.R. 1996. *Haematopus Ostralegus* in perspective: comparisons with other oystercatchers. pp. 251–285 in *The Oystercatcher: from Individuals to Populations*. J.D. Goss-Custard (ed.). Oxford University Press, Oxford.

Karl, J.W., P.J. Heglund, E.O. Garton, J.M. Scott, N.M. Wright & R.L. Hutto. 2000. Sensitivity of species habitat-relationship model performance to factors of scale. *Ecol. Appl.* 10: 1690–1705.

Lafferty, K.D., D. Goodman & C.P. Sandoval. 2006. Restoration of breeding snowy plovers following protection from disturbance. *Biodiv. & Conserv.* 15: 2217–2230.

Leseberg, A., P.A.R. Hockey & D. Loewenthal. 2000. Human disturbance and the chick-rearing ability of African Black Oystercatchers (*Haematopus moquini*): a geographical perspective. *Biol. Conserv.* 96: 379–385.

Lippitt, C.D., J. Rogan, J. Toledano, F. Saylgermano, J.R. Eastmana, V. Mastro & A. Sawyer. 2008. Incorporating anthropogenic variables into a species distribution model to map gypsy moth risk. *Ecol. Modelling* 210: 339–350.

Major, R.E. 1990. The effect of human observers on the intensity of nest predation. *Ibis* 132: 608–612.

Martinez, M.L., A. Intralawan, G. Vazquez, O. Perez-Maqueo, P. Sutton & R. Landgrave. 2007. The coasts of our world: Ecological, economic and social importance. *Ecol. Economics* 63: 254–272.

McGowan, C.P. & T.R. Simons. 2006. Effects of human recreation on the incubation behavior of American Oystercatchers. *Wilson J. Ornith.* 118: 485–493.

McGowan, C.P., T.R. Simons, W. Golder & J. Cordes. 2005. A comparison of American Oystercatcher reproductive success on barrier beach and river island habitats in coastal North Carolina. *Waterbirds* 28: 150–155.

Munoz, J. & A.M. Felicisimo. 2004. Comparison of statistical methods commonly used in predictive modelling. *J. Vegetation Sci.* 15: 285–292.

O'Brien, C.S., S.S. Rosenstock, J.J. Hervert, J.L. Bright & S.R. Boe. 2005. Landscape-level models of potential habitat for Sonoran pronghorn. *Wildlife Soc. Bull.* 33: 24–34.

Palomino, D. & L.M. Carrascal. 2007. Threshold distances to nearby cities and roads influence the bird community of a mosaic landscape. *Biol. Conserv.* 140: 100–109.

Phillips, S.J., R.P. Anderson & R.E. Schapire. 2006. Maximum entropy modeling of species geographic distributions. *Ecol. Modelling* 190: 231–259.

Prasad, A.M., L.R. Iverson & A. Liaw. 2006. Newer classification and regression tree techniques: Bagging and random forests for ecological prediction. *Ecosystems* 9: 181–199.

Pulliam, H.R. 1988. Sources, sinks and population regulation. *Am. Naturalist* 132: 652–661.

Pulliam, H.R. 2000. On the relationship between niche and distribution. *Ecol. Letters* 3: 349–361.

Rushton, S.P., S.J. Ormerod & G. Kerby. 2004. New paradigms for modelling species distributions? *J. App. Ecol.* 41: 193–200.

Safina, C. & J. Burger. 1983. Effects of human disturbance on reproductive success in the Black Skimmer. *Condor* 85: 164–171.

Schulz, R. & M. Stock. 1993. Kentish plovers and tourists – competitors on sandy coasts? *Wader Study Group Bull.* 68: 83–92.

Swets, J.A. 1988. Measuring the accuracy of diagnostic systems. *Science* 240: 1285–1293.

Thuiller, W., L. Brotons, M.B. Araujo & S. Lavorel. 2004. Effects of restricting environmental range of data to project current and future species distributions. *Ecography* 27: 165–172.

Toland, B. 1999. Nest site characteristics, breeding phenology, and nesting success of American Oystercatchers in Indian River County, Florida. *Florida Field Nat.* 27: 112–116.

Turgeon, K. & M.A. Rodriquez. 2005. Predicting microhabitat selection in juvenile Atlantic salmon *Salmo sala* by the use of logistic regression and classification trees. *Freshwater Biol.* 50: 539–551.

Usio, N., H. Nakajima, R. Kamiyama, I. Wakana, S. Hiruta & N. Takamura. 2006. Predicting the distribution of invasive crayfish (*Pacifastacus leniusculus*) in a Kusiro Moor marsh (Japan) using classification and regression trees. *Ecol. Res.* 21: 271–277.

Van der Zande, A.N. & T.J. Vestral. 1985. Impacts of outdoor recreation upon nest-site choice and breeding success of the Kestrel. *Ardea* 73: 90–99.

Verhulst, S., K. Oosterbeek & B.J. Ens. 2001. Experimental evidence for effects of human disturbance on foraging and parental care in oystercatchers. *Biol. Conserv.* 101: 375–380.

Virzi, T., J.L. Lockwood, R.G. Lathrop, Jr. & D. Drake 2008. *Predicting American Oystercatcher distribution in an urbanized coastal ecosystem using maximum entropy modeling.* Ph.D. Dissertation. Rutgers University, New Brunswick, NJ, USA.

Virzi T., J.L. Lockwood, D. Drake & T. Pover. 2010 In review. Conservation of American Oystercatchers *Haematopus palliatus* within an urbanized barrier island complex. *Bird Conserv. Int.*

Yalden, P.E. & D.W. Yalden. 1990. Recreational disturbance of breeding Golden Plovers *Pluvialis apricarius*. *Biol. Conserv.* 51: 243–262.

Zigler, S.J., T.J. Newton, J.J. Steuer, M.R. Bartsch & J.S. Sauer. 2008. Importance of physical and hydraulic characteristics to unionid mussels: a retrospective analysis in a reach of large river. *Hydrobiologia* 598: 343–360.