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Published By: The Waterbird Society

DOI: [http://dx.doi.org/10.1675/063.040.sp112](http://dx.doi.org/10.1675/063.040.sp112)

Predicting American Oystercatcher (Haematopus palliatus) Breeding 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 Maxent, 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), this technique was used to develop a predictive model for the realized niche and local breeding distribution of American Oystercatchers (Haematopus palliatus) in coastal New Jersey, USA. The transferability of the predictive model to locations outside training areas was examined in an effort to locate new breeding populations in previously unsurveyed areas. Initial model validation indicated that Maxent performed well, exhibiting good discrimination ability based on analyses of both training data (AUC = 0.95) and test data (AUC = 0.91). Ground surveys based on the final model located 185 previously unknown territorial pairs of American Oystercatchers, showing that Maxent was useful to locate new populations in alternative breeding habitats. However, when validated with an independent dataset, the Maxent model did not perform much better than random (AUC = 0.54), reporting high omission (0.76-0.93) and commission (0.40-0.83) error rates. The poor validation was attributed to source-sink dynamics rather than to errors in the modeling technique. Future researchers attempting to validate species distribution models with ground surveys should take into consideration metapopulation and source-sink theory in the design of surveys and interpretation of results. Received 1 October 2015, accepted 23 June 2016.

Key words.—American Oystercatcher, Haematopus palliatus, Maxent, model transferability, model validation, species distribution modeling.

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 (Raxworthy et al. 2003; Ficetola et al. 2007; Pawar et al. 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 and Guisan 2006; Elith et al. 2006; Hirzel et al. 2006; Peterson 2006). Species distributions may be modeled using presence-absence data, or presence-only data when absence data is unavailable. Recently, a presence-only modeling technique using a machine learning approach, Maxent, has gained popularity (Phillips et al. 2006). While the technique has been shown to be a useful modeling method to determine a species’ realized distribution (Rebelo and Jones 2010), there are several potential pitfalls with using presence-only data to model distributions that must be carefully considered when interpreting results (Yackulic et al. 2013).

Underlying the major issues concerning distribution modeling are the transferability
of models and model validation (or evaluation) (Peterson et al. 2007; Boitani et al. 2008; Loiselle et al. 2008; 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 (Guisan and Zimmerman 2000; Rebelo and Jones 2010).

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 and 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. 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, an important concept that is often ignored in species distribution models (Chefaoui and Lobo 2008; Lobo et al. 2010). 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 (Pulliam 2000; Soberon and Peterson 2005; Peterson 2006).

Clarification of the niche concept is considered one of the major challenges in species distribution modeling (Araujo and Guisan 2006), and is an especially important consideration in any post hoc 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 modeling method and explanatory variables chosen generate different predictions ranging between the potential and realized distributions for the species of interest (Chefaoui and Lobo 2008).

The scale at which the predictions are developed also plays an important role in deciding whether a species’ fundamental or realized niche is being predicted (Fielding and Bell 1997; Filz et al. 2013). 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 interspecific 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.

We examined some of the potential issues with species distribution modeling using the popular presence-only modeling technique, Maxent, to predict the breeding distribution of American Oystercatchers (Haematopus palliatus) in coastal New Jersey, USA. We used a small dataset of known breeding records collected at a local scale to model the species’ breeding distribution over a broader scale in an effort to predict the occurrence of American Oystercatchers in previously unsurveyed areas, and to evaluate our model’s performance with an independent dataset. The distribution of breeding 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 their range by the early 1900s due to habitat loss and commercial hunting, American Oystercatchers have recently expanded north along the Atlantic coast of the United
States (Mawhinney et al. 1999; American Oystercatcher Working Group et al. 2012). It was during this time that the species’ local breeding distribution began to change, possibly facilitating the range expansion (Humphrey 1990), with American Oystercatchers found using alternative habitats to breed throughout their range (Lauro and Burger 1989; Shields and Parnell 1990; McGowan et al. 2005; Sanders et al. 2008).

Understanding the current breeding distribution of American Oystercatchers is the first step toward 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. 2001, 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 American 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 American Oystercatcher populations within New Jersey; and 3) evaluate the model’s predictive capability using an independent dataset to validate model results.

**Methods**

**Study Area**

The present study was conducted along the Atlantic Ocean coast of New Jersey (Fig. 1). High density breeding areas where intensive surveys were conducted in alternative breeding habitats include: 1) Island Beach State Park located in Ocean County (39° 46’ N, 74° 5’ W); 2) the Holgate Division of the Edwin B. Forsythe National Wildlife Refuge also located in Ocean County (39° 30’ N, 71° 17’ W); and 3) Stone Harbor Point located in Cape May County (39° 1’ N, 74° 46’ W). The habitat available for breeding American Oystercatchers at Island Beach included 3.3 km of undeveloped barrier beach, a 1.6-km inlet beach along an artificial dike, approximately 197 ha of adjacent saltmarsh, and an 8-ha artificial dredge-spoil island located in Barnegat Bay. The habitat at Holgate included 6.0 km of undeveloped barrier beach, approximately 74 ha of saltmarsh located directly adjacent to the barrier beach strand, and a 5-ha naturally-forming inlet island located within Little Egg Inlet. The habitat at Stone Harbor included 1.8 km of partially developed barrier beach, approximately 23 ha of saltmarsh located directly adjacent to the barrier beach strand, a nearby 126-ha saltmarsh island, and an 11-ha naturally-forming inlet island located within Herford Inlet.

**Surveys**

Training data for our species distribution models were provided by two datasets of occurrence records for breeding pairs of American Oystercatchers (Table 1; Fig. 1). First, the New Jersey Division of Fish & Wildlife – Endangered and Nongame Species Program provided occurrence records for American Oystercatchers breeding on barrier beaches along the Atlantic coast of New Jersey. This dataset was limited to occurrence records on the barrier beach strand since they did not conduct systematic surveys for American Oystercatchers in alternative habitats. Second, we conducted independent surveys during the 2006 breeding season (March–July) for American Oystercatchers at three high density breeding areas located in southern New Jersey (Fig. 1). Our surveys were conducted on barrier beach strands and in all available alternative breeding habitats at sites. We defined alternative breeding habitats as follows: 1) saltmarsh habitat (Spartina sp. dominant) directly adjacent to barrier islands; 2) isolated saltmarsh islands in back-bay areas behind barrier islands; 3) natural inlet islands; and 4) artificial dredge-spoil islands. All habitat types were available at each site. 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 navigable shorelines and tidal creeks, and by walking line transects spaced 100 m apart in interior marsh areas. We identified all territorial pairs of American Oystercatchers (i.e., pairs with active nests, nest scrapes, or those exhibiting territorial behavior) and marked all nests/pairs located with a handheld GPS.

We conducted additional surveys 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. The validation surveys were conducted from 1 May to 15 June, which is the peak breeding season for American Oystercatchers in New Jersey (Virzi 2008). We selected random survey points in all potential American Oystercatcher breeding habitat (i.e., barrier beach and alternative habitats) along the New Jersey Atlantic coastline from Sandy Hook (40°
Figure 1. Map showing occurrence records for breeding pairs of American Oystercatcher 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 outlined in black.
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. Trained observers recorded the presence or absence of territorial pairs of American Oystercatchers in a 100-m radius around each random survey point, and all pairs located within a 200-m radius from a randomly selected subset of points (25%) twice to quantify detection probability \( (p) \) using an occupancy modeling technique (MacKenzie et al. 2006). This effort confirmed that a single point survey provided adequate detection of territorial pairs when present \( (p = 0.80) \).

Predictive Model

We chose to use a species distribution modeling approach developed in a machine-learning environment (Maxent Software; Phillips et al. 2006) to model American 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). Studies have shown that Maxent outperforms other presence-only modeling techniques (Phillips et al. 2006; Gibson et al. 2007; Papes and Gaubert 2007; Ward 2007), and performs well in comparison to a wide variety of other species distribution modeling techniques (Elith et al. 2006; Phillips et al. 2009; Hertz et al. 2014). However, there are several potential pitfalls to the technique stemming from sampling design and detectability issues that should be considered when interpreting results (Yackulic et al. 2013). 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. The background data provide “pseudo-absences” to create predictive models when true absence data are not available. The pseudo-absences are not meant to be implied absences; they are meant to provide a sample of the set of environmental or habitat conditions available to the species of interest in the study region (Phillips et al. 2009).

Our training data included 67 territorial pair occurrence records identified during our 2006 surveys, and our background data (pseudo-absences) included the recommended 10,000 points drawn randomly from our 2006 study areas using Hawth’s Analysis Tools for ArcGIS (Beyer 2004). This method for choosing pseudo-absences corrects for sampling bias by limiting the selection of background data to the area where occurrence data were sampled, assuming there is no bias in the occurrence data due to survey design (Phillips et al. 2009; Syfert et al. 2013). To reduce sampling bias in our occurrence data, all available habitats within our study area were surveyed with the same effort. Further, within our training dataset we randomly removed all occurrence records located within 200 m of each other to reduce over-fitting due to spatial autocorrelation (Dormann et al. 2007). We chose this distance based on our knowledge of local American 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). Convergence threshold refers to the point where model iterations are performed allowing models to converge, and regularization refers to model smoothing. Generally, increasing these values avoids creating over-complex models and thus reduces over-fitting of models. The default settings 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: linear, quadratic, product, threshold, hinge and discrete (Phillips and 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). Although model performance may be improved by species-specific calibration of model parameters, the default settings in Maxent have been shown to perform well (Radosavljevic and Anderson 2014).

Environmental Variables

Maxent required that we create a set of spatially explicit environmental variables as background data over which the training data were modeled (Table 2). Following the recommendations of Burnham and Anderson (2002), we selected an a priori set of environmental variables that we hypothesized would influence the occurrence of American Oystercatchers in the study region. We selected variables that we hypothesized would influence

Table 1. Summary of all American Oystercatcher occurrence records used as training and validation data in Maxent models.

<table>
<thead>
<tr>
<th>Habitat Type</th>
<th>Training Data</th>
<th>Validation Data</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>No. Pairs</td>
<td>% Total</td>
</tr>
<tr>
<td>Barrier Beach</td>
<td>38</td>
<td>56.7</td>
</tr>
<tr>
<td>Saltmarsh</td>
<td>22</td>
<td>32.8</td>
</tr>
<tr>
<td>Inlet Islands</td>
<td>3</td>
<td>4.5</td>
</tr>
<tr>
<td>Dredge-Spoil Islands</td>
<td>4</td>
<td>6.0</td>
</tr>
<tr>
<td>Total</td>
<td>67</td>
<td>100.0</td>
</tr>
</tbody>
</table>
American 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 (Rushton et al. 2004; Gibson et al. 2007), 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 to derive all of our environmental variables (Table 2). These data were used to classify habitat into the following 12 categories: 1) urbanized habitat; 2) common reed (*Phragmites australis*) dominant wetlands; 3) coastal forest; 4) mixed scrub/shrub wetlands; 5) barren land; 6) tidal waters; 7) smooth cordgrass (*Spartina alterniflora*) dominant high marsh; 8) saltmeadow cordgrass (*S. patens*) dominant low marsh; 9) vegetated dunes; 10) mudflats; 11) barrier island beaches; and 12) other beaches (e.g., inlet beaches and small, perimeter beaches on back-bay islands). These data were used directly as a categorical habitat variable in the Maxent models. We also used these data to create eight additional continuous variables used in the models. We rasterized the land use/land cover polygons in ArcGIS (Environmental Systems Research Institute 2007) using a 10-m cell size within an area of extent that included a 10-km buffer from the Atlantic coastline of New Jersey, and used Spatial Analysis Tools (focal analyses) to derive all continuous variables. All GIS-derived variables used the same cell size and area of extent, which was a requirement of the Maxent software.

Based on our knowledge of American Oystercatcher breeding ecology and observed localized distributional patterns at demographic study sites used to collect training data, we formulated the following *a priori* hypotheses about the effects of our environmental variables on American Oystercatcher distribution at a broader, regional scale:

1) Breeding American Oystercatchers were expected to be more abundant in alternative habitats such as saltmarsh and back-bay islands (i.e., natural inlet or artificial dredge-spoil 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 American Oystercatcher presence;

3) The probability of American 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) American Oystercatcher distribution was expected to be clumped near Atlantic Ocean inlets since the conditions near inlets are favorable for the development of appropriate foraging habitat; and

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

Maxent provides several outputs that offer alternative methods for analyzing the contribution of each environmental variable on the projected distribution. These include a heuristic estimate of the relative contribution that each variable has on the projected distribution, response curves to examine the direction and magnitude of variable contributions, and jackknife tests to examine the effects of environmental variables on the final model. Higher values for heuristic estimates indicate more contribution of variables to model outcomes. The jackknife tests provide a further indication of variable importance by testing for improvement in model performance after removing each variable individually and by running models with variables in isolation. Separate jackknife tests are conducted for training gain, test gain and area under the receiver operating characteristic curve for the Maxent model.

**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 (Swets 1988; Fielding and Bell 1997). Models are evaluated based on the area under the ROC curve (AUC), which ranges from 0-1. A score of one indicates perfect model discrimination, a score > 0.75 indicates good model discrimination, a score between 0.50-0.75 indicates that the model is performing better than random, and a score < 0.50 indicates poor model discrimination (Swets 1988; Elith et al. 2006). We recognize that using predefined benchmarks such as AUC scores to evaluate model performance may not always be best because many alternative species distribution models may produce similar results (Ashcroft et al., 2011), and results may be especially confounded if training data are imbalanced (Jimenez-Valverde and Lobo 2006).

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 (Pearce and Ferrier 2000; Elith et al. 2006). Until recently, validation of species distribution models with independent datasets was rare (Rebelo and Jones 2010; Filz et al. 2013; Syfert et al. 2013; Hertzog et al. 2014). To better evaluate model performance, rather than relying solely on internal cross validation in Maxent, we performed additional analyses using validation data obtained from our independent surveys conducted in 2007. Presence-absence data collected at 283 randomly selected sites in previously unsurveyed areas (i.e., areas outside training data sites) were compared to occurrence probability values at the survey sites as provided by the Maxent model results. We calculated ROC curves using the presence-absence data collected, which allowed us to compare AUC values derived from the validation data with the AUC from the final Maxent model. To calculate the ROC curves, we extracted the Maxent probability value at each random survey point, along with the mean and maximum values within a 110-m radius buffer around all survey points. We chose to include buffer values in our model validation since we expected the probability of American Oystercatcher presence to be dependent on the amount of suitable habitat available within a 110-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 (Fielding and Bell 1997; Anderson et al. 2003), which may be a better way to understand the reliability of model results (Lobo et al. 2010). We derived several confusion matrices using the different methods to extract Maxent values from our results as described above, and we applied three different thresholds to dichotomize the continuous distribution values (0.30, 0.50 and 0.70). We chose a range of threshold values because reliance on a fixed threshold value may lead to spurious results, especially when there are unbalanced samples (Liu et al. 2005), which is the case with our validation data. Finally, we calculated Cohen’s kappa values for validating the final Maxent model since this statistic is widely used in presence-absence modeling, tends to be more forgiving when prevalence is low, and is less affected by zero values in the confusion matrix (Manel et al. 2001). Similar to AUC values, kappa values range from 0-1, with values of one representing perfect model discrimination and values < 0.50 indicating poor discrimination. All statistical analyses were performed in R (R Development Core Team 2012).

Results

Predictive Model

The Maxent model predicted a high probability of American Oystercatcher presence in alternative breeding habitats removed from barrier island beaches in New Jersey (Fig. 2), especially in the southern regions of the State 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). In general, maps produced by the Maxent model output provided predictions that were useful to locate new American Oystercatcher populations. Ground surveys conducted at 283 random sites, selected based on results of the final Maxent model, identified 185 previously unknown territorial pairs of American Oystercatchers in coastal New Jersey. However, final validation of the Maxent model with the independent dataset proved difficult due to several potential sources of error described in greater detail below.

Explanatory Variables

The heuristic estimates (Table 2) indicated that distance from tidal waters had
the greatest influence on predicted American Oystercatcher distribution with probability of presence substantially higher in areas closer to tidal waters. The heuristic estimate also indicated that habitat classification had a very large influence on
predicted American Oystercatcher distribution. The response curve for the habitat classification variable (Fig. 4) indicated American Oystercatchers preferred low marsh (S. alterniflora dominant marsh), vegetated dunes, barrier beaches and other beaches, including those found on inlets, natural or artificial islands and saltmarsh margins (variables 8, 9, 11 and 12, respectively). Sandy beaches found in alternative habitat had by far the highest probability of American Oystercatcher presence (variable 12), as we hypothesized. While the availability of sand substrates appeared to increase the probability of American 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 classification (Fig. 5).
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 American Oystercatchers select breeding habitat in close proximity to foraging areas. The jackknife test of AUC also indicated that the probability of American 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 (Fig. 5).

Model Validation

Results of independent American Oystercatcher surveys conducted along the New Jersey Atlantic coastline during 2007 indicated that most breeding American Oystercatchers were distributed in alternative habitats as the Maxent model suggested (Table 1; Fig. 6). 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. Cohen’s kappa values were substantially < 0.50 regardless of the threshold used to calculate values, further indicating poor model discrimination (Table 3). Thus, while maps produced as output by the Maxent model appear to correctly show areas in alternative breeding habitat as having high occurrence probabilities, the validation data contradict this result when examined at a localized scale.

To further examine the potential 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). Results based on a threshold value of 0.30 are not reported; however, the results were similar to those based
Figure 5. Jackknife tests of training gain (gain is related to deviance), test gain and AUC (area under the receiver operating characteristic (ROC) curve) for the Maxent model.
on the other thresholds. 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.

Figure 6. New Jersey American Oystercatcher distribution based on results of 2007 validation surveys. Data presented includes all territorial pairs located during surveys.
Table 3. Confusion matrices and error rates derived from presence/absence data collected during 2007 American Oystercatcher validation surveys. Matrices based on three methods used to extract Maxent probability values and two thresholds. AUCmax = area under the receiver operating characteristic curve (AUC) based on maximum Maxent probability value within 110-m radius of points; TP = true positives; FN = false negatives; TN = true negatives; FP = false positives; OE = omission error rate; CE = commission error rate; K = Cohen’s kappa.

<table>
<thead>
<tr>
<th>Measure</th>
<th>Threshold</th>
<th>TP</th>
<th>FN</th>
<th>TN</th>
<th>FP</th>
<th>OE</th>
<th>CE</th>
<th>K</th>
</tr>
</thead>
<tbody>
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<td>Point</td>
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<td>9</td>
<td>37</td>
<td>203</td>
<td>34</td>
<td>0.80</td>
<td>0.79</td>
<td>0.05</td>
</tr>
<tr>
<td>Mean</td>
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<td>6</td>
<td>40</td>
<td>220</td>
<td>17</td>
<td>0.87</td>
<td>0.74</td>
<td>0.07</td>
</tr>
<tr>
<td>Max</td>
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<td>35</td>
<td>185</td>
<td>52</td>
<td>0.76</td>
<td>0.83</td>
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<td>0.87</td>
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</tr>
<tr>
<td>Mean</td>
<td>0.70</td>
<td>3</td>
<td>43</td>
<td>235</td>
<td>2</td>
<td>0.93</td>
<td>0.40</td>
<td>0.09</td>
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<tr>
<td>Max</td>
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<td>38</td>
<td>219</td>
<td>18</td>
<td>0.83</td>
<td>0.69</td>
<td>0.12</td>
</tr>
</tbody>
</table>

**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 American Oystercatcher presence in alternative breeding habitats away from the barrier beach strand, which is the historically preferred breeding habitat for the species. Ground surveys based on our model located 185 previously unknown territorial pairs of American Oystercatchers in alternative habitats in coastal New Jersey, which more than doubled the estimate of the State’s breeding population. As a result of our surveys, we now estimate that 81% of the New Jersey American Oystercatcher population breeds in alternative habitats away from the barrier beach strand. However, within the alternative habitats many of these American Oystercatchers were found at sites with lower predictive values, indicating there may be other factors influencing local distributional patterns.

Visual inspection of the Maxent model output maps indicated that American Oystercatchers were less likely to be found in areas with a high degree of urbanization; however, urbanization variables were of low importance in the final model. Still, urbanization may partially explain the low probability of occurrence reported in the northern part of the New Jersey coast, which is the most highly developed coastal area in the State, due to its effect on other environmental variables that are more important to American Oystercatchers. For example, the habitat surrounding Barnegat Bay has been severely altered (especially in the north) with over 70% of the adjacent upland shoreline developed and 36% of the total shoreline bulkheaded (Lathrop and Bognar 2001). This activity limits the amount of alternative breeding and foraging habitat available to American Oystercatchers in this region. At the local scale, American 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 (site-level), we saw that the predictive capability of the final Maxent model was poor. Regardless of the method or thresholds 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. 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 (Araújo et al. 2005). Other attempts to validate Maxent models with independent data have also proven difficult (Filz et al. 2013; Hertzog et al. 2014). 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; 3) the current distribution may not reflect the realized niche due to disequilibrium with environmental conditions as the species undergoes a range expansion; and 4) the models may accurately predict the realized niche but American Oystercatchers are using 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 American 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. High AUC values such as those observed in our Maxent model may not necessarily indicate good model performance, especially if training data were sampled disproportionately (Smith 2013). However, we took measures to reduce this potential error in our survey design for our occurrence data and 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 avoiding 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 (Dudík 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 the size of the habitat features such as small sand banks or wrack deposits were below the resolution of the land cover dataset; therefore, these areas should have received higher predicted suitability values in our final model. The occurrence of American Oystercatchers in these areas led to misclassified false negatives in our confusion matrices. Resolution in GIS data is known to cause problems when attempting to validate models with independent data collected at different scales (Filz et al. 2013). Inclusion of finer scale land cover GIS data 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.

The goal of our distribution model was to predict the realized niche of the American Oystercatchers in New Jersey, 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). However, the current distribution may not reflect the species’ niche because it may not be in equilibrium with the distribution of environmental conditions used to model the distribution (Yackulic et al. 2015). This disequilibrium may be particularly common at the edge of a species’ range, and rates of local colonization and extinction during range expansion can produce substantial temporal variation in occupancy-environment relationships (Yackulic et al. 2015). Still, Maxent has been shown to predict a species’ realized niche well, especially when attention is paid in the selection of pseudo-absences to reduce sampling bias as done in this study (Lobo et al. 2010). We
feel that our Maxent model predicted the realized niche (highly suitable areas) well for American Oystercatchers, supported by the observation that these areas had much higher densities of territorial pairs (Virzi 2008). However, our independent surveys indicated that American Oystercatchers were also widely distributed in areas predicted to be unsuitable.

Even if we assume that our Maxent model is accurately predicting the realize niche for American Oystercatchers in New Jersey, our sampling design for both training and validation data should be considered in the interpretation of model results because of the potential bias that could result due to imperfect detection not being considered in our models (Miller et al. 2015; Yackulic et al. 2015). Detection probability for our training data was likely near perfect because: 1) our repeated survey methods during intensive demographic research provided an almost complete census of study areas; and 2) we ensured that all potential breeding habitats were surveyed with similar effort. However, detection probability for our validation data was less than one, and this imperfect detection was not included in our models. Further, we did not model heterogeneity in detection among habitat types, which could lead to underestimation of occupancy in some habitats (Miller et al. 2015). While we do not expect that detection probability varied among sites in our study, we caution that the influence of imperfect detection and unmeasured heterogeneity could partially explain the poor validation of our Maxent model with the independent dataset.

In the absence of significant data errors in our models, it is possible that the final model accurately predicts the realized niche, but American Oystercatchers are using unsuitable (sink) habitat. 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 et al. (1995) showed a despotic distribution for the Eurasian Oystercatcher (Haematopus ostralegus) 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. 6), it is clear that American Oystercatcher occurrences in unsuitable habitat are often located near areas with high suitability values. We interpret this as evidence that American Oystercatchers in New Jersey are exhibiting a similar despotic distributional pattern as reported for the Eurasian Oystercatcher (Ens et al. 1995). Virzi et al. (2016) showed that most American 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 lower reproductive output indicating these areas may be acting as sink habitat. The high density of territorial pairs in areas with high suitability values may also indicate that these areas are saturated with American Oystercatchers, forcing many individuals to breed in nearby low-lying saltmarsh sink habitat due to habitat limitations. Given the condition of coastal ecosystems in New Jersey, it is not surprising that such a high proportion of the known American 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 predicted American Oystercatcher presence in areas where they were not observed to occur in our independent validation surveys (i.e., the model overpredicted suitable breeding habitat area). This suggests that there may be additional factors not included in our models that may
be further influencing the local American Oystercatcher distribution. For example, it is possible that human disturbance on breeding grounds, which was not included in our models, may be keeping American Oystercatchers from using highly suitable breeding habitat (Virzi 2010). 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 and Vestral 1985; Yalden and Yalden 1990). Another plausible explanation, however, is that American Oystercatchers in New Jersey simply are not using all available habitat during the recent range expansion, creating a temporal disequilibrium in occupancy patterns (Yackulic et al. 2015). Colonization of new habitats (e.g., dredge-spoil islands) is likely very important during range expansions; however, we would still expect American Oystercatchers to first colonize barrier beach habitat since this historically has been the preferred breeding habitat for the species. Further, Yackulic et al. (2015) indicate that case studies show that species were at or near equilibrium two decades after first arriving at a new location, which suggests that the New Jersey American Oystercatcher population should have had enough time since first recolonizing the State more than two decades ago to reach equilibrium.

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 American 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 American Oystercatcher population breeds in alternative habitats (Traut et al. 2006). There could be severe consequences to the overall American Oystercatcher population along the Atlantic coast of the United States if the species is indeed expanding its range northward and concurrently shifting its breeding habitat into sink habitat. Further research is needed to understand American Oystercatcher productivity in alternative breeding habitats and to identify small, isolated areas that may act as local source populations. 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. Finally, survey design should include methods to enable estimation of heterogeneity of detection probability among habitat types, and imperfect detection should be incorporated into distribution models.

Acknowledgments

We would like to thank David Ehrenfeld for his valuable input. The Grant F. Walton Center for Remote Sensing and Spatial Analysis (CRSSA) provided all computing resources. We are indebted to all those in the CRSSA lab who helped us along the way including Jim Trimble, John Bogner, Scott Haag, Mike Mills, Inga Parker, Caroline Phillipuk, Zewei Miao and Aaron Love. Thanks to Larry Niles, Dave Jenkins, Todd Pover and Jim Merritt for all of their assistance and support. We also thank the two anonymous reviewers for their comments on the manuscript. Financial support came from the New Jersey Division of Fish and Wildlife – Endangered and Nongame Species Program and the Edwin B. Forsythe National Wildlife Refuge. A special thanks to Jeff Faust for helping with American Oystercatcher surveys. And finally, thanks to Kristen Faust who spent countless hours in the field.

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