Assessing the Impacts of Sea-Level Rise on Piping Plovers at Assateague Island, Virginia and Maryland.



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Chapter 1: Project introduction and objectives

Project Introduction: The purpose of this project was to provide biologists and managers along the Atlantic coast with tools to predict the effects of accelerating sealevel rise on the distribution of piping plover breeding habitat, to test those predictions, and to feed results back into the modeling framework to improve predictive capabilities. Our goals were to provide short-term (i.e., over project life) results related to the effects of sea level rise on piping plover breeding habitat at Assateague Island and to use these results to ultimately (i.e., longer term, during and beyond project life) inform a coast-wide assessment of threats from sea-level rise and related habitat conservation recommendations that can be implemented by land managers and inform recommendations to regulators. We also sought to test several case studies incorporating explicit measures to preserve resilience of piping plover habitat to sea level rise into management plans for Assateague Island National Seashore (ASIS) on Assateague Island.

Accomplishment of the project required integration of two parallel tasks by Virginia Tech and the USGS Sea Level Rise Hazards Project. The first task, conducted by Virginia Tech as lead, utilized data on piping plover (*Charadrius melodus*) habitat preference for, and utilization of, topographic, hydrodynamic, and vegetation regimes to construct a model of piping plover nest site selection that is quantitatively tied to measurable physical variables. The second task, conducted by USGS as lead, developed a model of barrier island geomorphology and its relation to changes in sea level and storminess. These two models were coupled to each other and to a previously published (Gutierrez et al., 2011) model of the effects of sea level rise on shoreline change. These 3 linked models were evaluated against historical data to determine hindcast skill and then used to forecast future conditions of shoreline change, geomorphology, and piping plover nest site selection.

<u>Project Objectives</u>: Given the above project purpose, our specific objectives were as follows.

- 1. Assess the literature and compile historical data on piping plover nest site selection from Assateague Island in order to develop and test a model of piping plover nest site selection that could be linked to island geomorphology and shoreline change.
- 2. Coordinate with USGS Sea Level Rise Hazards project in the development of the island geomorphology model and linkage of the plover nest selection model to the geomorphology and shoreline change models.
- 3. Assess the literature and interact with managers in order to develop a set of sealevel rise and management scenarios to forecast related to future nest site conditions of piping plovers on Assateague Island.

4. Test the individual and linked models in hindcast scenarios, refine models, and then forecast future piping plover nest site conditions on Assateague Island under a set of sea-level rise and management scenarios.

In this final report, we report the outcomes of our work on this suite of objectives as follows.

- 1. Modeling methods and results, related to objectives 1-4, are presented in chapters 2 and 3 as the methods and results sections of 2 peer-reviewed scientific papers.
- 2. A strategy synthesizing information about the effects of sea-level rise on piping plover breeding habitat, and articulating sea-level rise habitat conservation recommendations, is presented throughout the document as follows. The introduction and discussion sections of chapters 2 and 3 provide information about the effects of sea-level rise on piping plover breeding habitat as summarized from both peer-reviewed literature and agency reports, and as demonstrated through our modeling efforts. Finally, chapter 4 of this document provides a summary of conservation recommendations from our work and recommendations for future work.
- 3. We assessed the effects of 2 future rates of sea-level rise, and 2 potential management strategies in response to that sea-level rise, on future resilience of piping plover habitat in chapter 3 and summarize our findings in chapter 4.
- 4. Chapter 5 provides a summary of scientific papers in press or in review, and presentations given at scientific meetings, related to this project.

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A Bayesian network approach to predicting nest presence of the federally-threatened piping plover (*Charadrius melodus*) using barrier island features[†]

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ABSTRACT

Sea-level rise and human development pose significant threats to shorebirds, particularly for species that utilize barrier island habitat. The piping plover (Charadrius melodus) is a federally-listed shorebird that nests on barrier islands and rapidly responds to changes in its physical environment, making it an excellent species with which to model how shorebird species may respond to habitat change related to sea-level rise and human development. The uncertainty and complexity in predicting sea-level rise. the responses of barrier island habitats to sea-level rise, and the responses of species to sea-level rise and human development necessitate a modeling approach that can link species to the physical habitat features that will be altered by changes in sea level and human development. We used a Bayesian network framework to develop a model that links piping plover nest presence to the physical features of their nesting habitat on a barrier island that is impacted by sea-level rise and human development, using three years of data (1999, 2002, and 2008) from Assateague Island National Seashore in Maryland. Our model performance results showed that we were able to successfully predict nest presence given a wide range of physical conditions within the model's dataset. We found that model predictions were more successful when the ranges of physical conditions included in model development were varied rather than when those physical conditions were narrow. We also found that all model predictions had fewer false negatives (nests predicted to be absent when they were actually present in the dataset) than false positives (nests predicted to be present when they were actually absent in the dataset), indicating that our model correctly predicted nest presence better than nest absence. These results indicated that our approach of using a Bayesian network to link specific physical features to nest presence will be useful for modeling impacts of sea-level rise or human-related habitat change on barrier islands. We recommend that potential users of this method utilize multiple years of data that represent a wide range of physical conditions in model development, because the model performed less well when constructed using a narrow range of physical conditions. Further, given that there will always be some uncertainty in predictions of future physical habitat conditions related to sea-level rise and/or human development, predictive models will perform best when developed using multiple, varied years of data input.

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1. Introduction

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Many shorebird species are threatened by the impacts of sealevel rise and human development on their habitats, particularly their low-lying habitats found on barrier islands. Barrier islands are long, narrow landforms that fringe mainland coasts, and are bounded on one side by an ocean, gulf, or sea, and on the other side by a lagoon that abuts the mainland (Davis and FitzGerald, 2004). Along the US Atlantic Coast, barrier islands stretch from Maine to Florida, or some 3700 km and encompass an area of 6800 km² (Zhang and Leatherman, 2011). These barrier islands provide vital







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breeding habitat for many shorebird species, including the piping plover (*Charadrius melodus*), a shorebird that was federally listed as threatened along the US Atlantic Coast under the US Endangered Species Act in 1986 (US Fish and Wildlife Service, 1985).

Piping plover nest site selection is driven by the need to select habitat features that maximize access to reliable food sources and minimize flooding from overwash or storms, predation, and intraspecific/interspecific competition for food resources. A balancing of these selective forces results in plovers typically nesting on flat, open, low-lying dry sand or pebble beaches (Houghton, 2005) with clumped sparse vegetation (Cohen, 2005; Cohen et al., 2008), adjacent to moist substrate habitat (MOSH) where plovers feed (Cohen, 2005), near dunes (Burger, 1987; Powell and Cuthbert, 1992), and away from the high tide boundary (Cohen, 2005).

Piping plovers select nest sites based on the proximity to MOSH where they feed. On barrier islands, MOSH is most commonly associated with bayside or sound-side low wave energy beaches (Cohen, 2005; Cohen et al., 2009; Keane, 2002) but is generally characterized by habitat features such as intertidal mud flats or sand flats, and ephemeral pools that are rich in preferred prey resources (Elias and Fraser, 2000; Fraser et al., 2005; Keane, 2002; Patterson et al., 1991). Access to a reliable food source is such a vital determinant of nest site selection that piping plovers preferentially nest adjacent to MOSH (Loegering and Fraser, 1995) even when presented with physical barriers that prevent chicks from accessing the MOSH (Fraser et al., 2005; Keane, 2002; Loegering and Fraser, 1995); Patterson et al., 1991).

Piping plovers select bayside or sound-side habitat for nesting not only because of its likely greater proximity to MOSH, but also for the increased protection from flooding, as bayside habitat is farther from oceanfront wave action than ocean-side habitat, and is often separated from the oceanfront by dunes. Plovers that nest on ocean-side beaches typically place nests above the daily and spring high-tide flood levels and close to dunes to avoid overwash events (Maslo et al., 2011). The areas of bare sandy, pebble, or gravel substrate pocketed with clumps of vegetation that typically characterize plover nesting sites offer camouflage from predators for adults and their eggs and chicks (Maclvor, 1990; Maslo et al., 2011; Patterson et al., 1991).

Despite our extensive knowledge on the relationship between piping plover nest site selection and physical features of barrier islands, there has been little work done to explicitly link how sea-level rise or human-induced alterations in barrier island geomorphology affect the physical habitat features selected by nesting piping plovers. Barrier islands' positions between the ocean and mainland make them particularly attractive for commercial and residential real estate while their generally low elevations make them highly vulnerable to the effects of sea-level rise; these conflicting attributes often result in the demand for shoreline protection measures that may actually degrade habitats and resilience in the long-term (Feagin et al., 2005; Houston, 2008; Schlacher et al., 2007; Weinstein et al., 2007). Recent studies on the effects of sealevel rise on barrier islands have emphasized the need for further research on the uncertainty that these anthropogenic factors introduce into the complex process of modeling sea-level rise effects on habitats and species (Chu-Agor et al., 2012; Convertino et al., 2011; Seavey et al., 2011).

Piping plovers respond rapidly to physical changes in their environment (Cohen et al., 2009; Kumer, 2004; Schupp et al., 2013) and are thus an ideal indicator species to model the effects of sea-level rise and human development on barrier island habitat and shorebirds, as has been done in previous studies (Aiello-Lammens et al., 2011; Seavey et al., 2011). The models used in these previous studies delineated general shorebird habitat based on historical nesting locations, and applied sea-level rise and/or human development scenarios to those known nesting habitats. To accurately predict how sea-level and human development driven changes in barrier island physical features will impact piping plovers, we need to link piping plover habitat selection to those physical features that will be altered by these processes. Our objective in this paper was to develop and test a model that links piping plover nest presence or absence to these physical features of their nesting habitat using data readily available across the breeding range via remote sensing tools and minimal on-the-ground effort for beach managers.

We used a Bayesian network (BN) modeling framework to accomplish our objective. A BN is a type of directed graphical model with nodes that represent variables and arcs (i.e. arrows) that represent conditional dependencies among variables. The graphical structure of BN's provide a clear representation of the links among variables that facilitates their use as a resource management tool across multiple disciplines and stakeholder groups (Uusitalo, 2007). The conditional probability distributions for each variable are derived using Bayes' Theorem, and thus BNs can be readily updated as new information becomes available and are easily adapted to a variety of circumstances. Furthermore, the conditional probability distributions can be derived and updated using various forms of data, including data with missing observations, thus allowing uncertainty to be propagated through the network (Koller, 2009). Our ultimate aim in developing this model was to provide a tool for managers to predict piping plover nest presence or absence under various scenarios of sea-level rise and human development. The BN's explicit graphical representation, flexibility, adaptability, and incorporation of uncertainty provided us with the ideal framework with which to build such a model.

In this paper we present how we constructed a BN (Koller, 2009; Pearl, 1988) to link piping plover nest presence to the physical features of a barrier island in Assateague Island National Seashore (ASIS), MD, based on data collected in 1999, 2002, and 2008. We then assess how well the model predicted nest presence or absence within and across years, and how varying ranges of the specific physical features influenced the likelihood of predicting plover nest presence or absence. Finally, we discuss how this model can be simplified and applied to other coastal sites and used to predict future changes in piping plover populations related to sea-level rise and human development.

2. Methods

2.1. Study site and model variables

The study area encompassed the northern 10 km of ASIS, hereafter 'the North End'. ASIS is located on Assateague Island, Maryland, a 58-km barrier island off the coasts of Maryland and Virginia, US (38°05' N, 75°12' W, Fig. 1). Assateague Island supports a mosaic of habitats ranging from marsh and mudflats on the bayside, to coniferous and deciduous forest in the interior, and dunes and sandy beach on the ocean-side. As a barrier island, Assateague Island has low elevations with a mean cross-shore elevation of approximately 4 m above mean sea level (all elevations in this study referenced to North American Vertical Datum 1988 mean sea level, 0.34 m NAVD88) and narrow widths ranging from approximately 220-4500 m. The North End is particularly low lying and narrow, with a mean cross-shore elevation of approximately 1 m above mean sea level and widths ranging from approximately 260-700 m, and has held more than 90% of the total Maryland piping plover nesting population since the National Park Service (NPS) began monitoring plover nesting populations here in 1992.

The North End's particularly low elevation and narrow width compared to the rest of Assateague Island make this area especially vulnerable to storm damage. Severe winter storms in late January and early February 1998 washed over the entire width of the island



Fig. 1. We used piping plover (*Charadrius melodus*) nest locations and random points without nests, and data on physical features, from the northern 10 km of Assateague Island National Seashore, MD, USA, to construct a Bayesian network to predict the probability of nest presence and absence. A human modification, a low foredune constructed in 1998 and composed of coarse sediment mined offshore, is also depicted. This foredune played a significant role in modifying the habitat on the North End over time (see Schupp et al., 2013), which resulted in markedly different environments from one study year to the next.

along a 2.4 km section of the North End used by piping plovers as nesting habitat (Sallenger et al., 1999; Schupp et al., 2013). The North End's particularly low elevation and narrow width is perpetuated by an interruption of alongshore sediment deposition caused by a permanent jetty constructed to maintain the Ocean City Inlet to the north after this inlet was created by a hurricane in 1933 (Dean and Perlin, 1977; Rosati and Ebersole, 1997). To compensate for the interruption in sediment and to prevent particularly vulnerable sections of the North End from breaching during severe storm events, the US Army Corps of Engineers (USACE) constructed a low foredune after the storms in 1998 along the length of the 2.4 km section that was washed over during the severe storm events of that same year (USACE, 1998). The foredune (Fig. 1) was constructed to a maximum height of 3.05 m using material dredged from an offshore shoal. The foredune's design was meant to allow for climatic forces and storm effects that would gradually erode the foredune while preventing breaching during severe storm events until a more permanent restoration plan could be devised to mitigate the effects the inlet had on the North End (USACE, 1998). This comprehensive restoration plan incorporated a one-time replacement of 15% of the volume of sediment lost to the inlet since 1934 and a biannual replenishment of the sediment supply that continues to be interrupted by the inlet. The one-time replacement was conducted in 2002 and replaced approximately 1.4 million m³ of sand across a 10.5 km alongshore distance of the North End, widening the beach along this length by approximately 30 m. The bi-annual replenishment began in 2004 and continues through present, biannually replenishing approximately 144,000 m³ of sediment to the nearshore of the North End adjacent to the 2.4 km section where the low foredune was constructed (Schupp et al., 2013; USACE, 1998). The height of the foredune resulted in a lack of overwash despite increased hurricane activity in subsequent years, resulting in widespread vegetation encroachment behind the foredune (Carruthers et al., 2011, 2013; Schupp et al., 2007, 2013; Fig. 2).

Piping plovers tend not to nest in thick vegetation because they cannot see approaching predators and also because their flightless chicks have difficulty navigating through dense vegetation to reach foraging sites (Cohen et al., 2009). Thus vegetation growth over time rendered many of the areas used by piping plovers before the 1998 storms and foredune construction unsuitable for nesting.

We used data on piping plover nest locations, random points, and physical features from nest and random points from the nesting seasons of 1999, 2002, and 2008. While the NPS has been collecting data on breeding piping plovers since 1992, habitat data were not available for every year. These three years were selected for analyses because there were data available for a large proportion of the physical features in our model.

Geographic coordinates of all piping plover nest locations were recorded by NPS staff immediately upon finding a nest, using a backpack Global Positioning System (GPS; make and model unrecorded) with a horizontal accuracy of ± 5 m in 1999 and 2002, and a Trimble Pathfinder ProXH DGPS with a horizontal accuracy of ± 1 m in 2008. We generated an equal number of random points as the number of actual plover nests for each year using ArcGIS10. Random points were defined as being without a nest in sites with a vegetation density and composition amenable to plover nesting (e.g., dense woody vegetation was excluded because piping plovers do not nest in forested habitats).

Data on physical features of both nest points and random points were derived from airborne elevation data, aerial photo images



Fig. 2. Distribution of piping plover (*Charadrius melodus*) nests and vegetation types (sparse, herbaceous, woody) recorded by National Park Service staff in their habitat maps in 1999 (a), 2002 (b), and 2008 (c) on the North End of Assateague Island National Seashore, MD, USA. The Atlantic Ocean is on the east side of the island while the Sinepuxent Bay is on the west side of the island. The section depicted here is the area immediately surrounding a low foredune constructed in 1998 that played a significant role in modifying the habitat on the North End over time (see Schupp et al., 2013) and is also where a majority of piping plovers nested from year.

of the North End (Bonisteel et al., 2009; Brock et al., 2002), and field-constructed habitat maps. NPS staff created habitat maps by walking boundaries of vegetation types defined as sparse (continuous vegetation density <20% within at least 25 m^2), herbaceous (continuous vegetation density >20% within at least 25 m^2), and woody (areas of woody shrubs and trees that were recognizable from an unspecified distance) using the same GPS units as described above. Boundaries that were not walked due to time and resource constraints were delineated by park staff using aerial photographs for each respective year (Schupp et al., 2013). We derived the following 12 variables for our BN (Fig. 3):

Nest attempt response variable: binary variable indicating whether a location was a piping plover nest or a random point.

Beach width: the width (m) of the beach at the location of the nest or random point, calculated as the horizontal distance between the dune toe (the low elevation point at the base of the dune) position and the position of the mean low tide water boundary (MLW). The beach width, particularly along the 2.4 km section where the foredune was constructed, is artificially enhanced by the additional bi-annual sediment input from the comprehensive restoration plan (described in the study site section).

Distance to dune crest: the distance (m) of each nest or random point to the dune crest (the high elevation point at the top of the dune, Stockdon et al., 2007, 2009). Dune crest points were converted to a line in ArcGIS10, and the perpendicular distance of this line to each nest and random point without nest was calculated using the Near Tool in ArcGIS10.

Distance to dune toe: the distance (m) of each nest or random point to the dune toe (i.e. break in slope at the base of the dune; Stockdon et al., 2007, 2009). Dune toe points were converted to a line in ArcGIS10, and the perpendicular distance of this line to

each nest and random point was calculated using the Near Tool in ArcGIS10.

Distance to mean high water (MHW) bay: the distance (m) of each nest or random point to the MHW tideline on the mainland side (i.e., backshore) of the barrier island. The backshore boundary was derived by manipulating the lidar datasets. Specifically, the National Oceanographic and Atmospheric Administration's VDatum software (Yang et al., 2008) was used to adjust the elevation data with respect to local MHW. From these data, a MHW contour was defined in ArcGIS10 using the Contour Tool and the perpendicular distance of this line to each nest and random point was calculated using the Near Tool. There were cases where the lidar data along the backshore was not of sufficient resolution to define a MHW contour. In these cases, either the 2008 backshore or the backshore derived from a 2003 aerial photo was used to approximate this shoreline, depending on which of these sources most closely approximated the MHW contour. The derived backshore contour was also double-checked against aerial photographs for the year corresponding to the lidar dataset to verify that it approximated the visible coastline for that year.

Distance to mean high water (MHW) ocean: the distance (m) of each nest or random point to the MHW tideline on the ocean-facing shore of the barrier island. This boundary was derived from lidar datasets as the line on the topographic surface that intersects MHW, adjusting for regional tidal datum elevation estimates (Stockdon et al., 2002; Weber et al., 2014). MHW ocean points were converted to a line in ArcGIS10, and the perpendicular distance of this line to each nest and random point was calculated using the Near Tool in ArcGIS10.

Distance to mean low water (MLW) bay: the distance (m) of each nest or random point to the MLW tideline on the backshore, derived



Fig. 3. Conceptual diagram illustrating the features we used to define the 12 physical and site fidelity variables in our Bayesian network, including the distances to features. MHW and MLW are the mean high water and mean low water boundaries, respectively. All distances, beach widths, and point elevations were calculated in meters. Distances were calculated from points to features, and beach width, elevation, slope, and vegetation were defined at points. Site fidelity represents whether a point was within 75 m of a nest from the previous year. Slope is the mean slope of a 5 m radius around the point. Points represent nests and random samples.

using the same procedure as for distance to MHW bay described above. The area between the MLW and MHW tideline on the backshore of the North End can be highly variable, whereas there is little variation in the area between the MLW and MHW tideline on the ocean-facing shore on the North End. Therefore, distance to the MLW ocean-facing shore was not included as a variable in the model.

Distance to moist substrate habitat (MOSH): MOSH was identified by conducting a supervised habitat classification in ArcGIS10, using the Maximum Likelihood Classification tool to classify color infrared (CIR) aerial photos of the study area. The classified regions were then used to identify and create polygons corresponding to different substrates on the barrier island. For areas where MOSH was identified and correlated to a specific CIR class, comparisons were made with aerial photographs to confirm these designations. Once defined, the shortest perpendicular distance (m) from the MOSH contour to each nest or random point was calculated using the Near Tool in ArcGIS10. Data for this variable were extracted for 2008 only, because infrared aerial photos were only available for that year.

Elevation: vertical height (m) above mean sea level calculated using the Extract Values to Points Tool in ArcGIS10 from lidar datasets for each nest and random point.

On Foredune: binary variable specifying whether nests and random points were located on or off the foredune constructed in 1998. The edge of the foredune was based on an outline that was created by NPS staff walking the boundary of the foredune using the same GPS unit as was used to create habitat maps. This foredune boundary was walked in 1998, 2002, and 2006. To define nests and random points that were on or off the foredune in 1999, we used the 1998 boundary. For 2002 nests and random points, we used the 2002 boundary, and for 2008 nests and random points, we used the 2006 boundary.

Site fidelity: binary value specifying whether nests and random points were within or outside of a 75 m radius around a nest location from the previous year. A distance of 75 m was selected based on long-term monitoring of nest locations and intra-year movements of color-marked piping plovers on the Missouri River (Friedrich et al., 2014).

Slope: a slope surface grid was generated using lidar datasets for each year and the Slope Tool in ArcGIS10. The Zonal Statistics Tool in ArcGIS10 was then used to pass the nest or random points, buffered by a 4 m radius, through the slope grid to obtain the mean slope (%) at the nest or random point.

Vegetation: variable that designated the general type and density (sparse: <20%, or herbaceous: >20% continuous ground cover within a minimum area of 25 m^2) of vegetation at the nest or random point. There were no nests or random points in woody vegetation, so this category was excluded. Vegetation data and categories were obtained from the ground-based habitat maps created by the NPS (see Section 2.1 and Schupp et al., 2013).

The number of nest and random points varied by year and among variables due to variability in the data layers' coverage and quality. For example, in 1999, data for distance to dune crest were complete with a total of 146 values, however several beach width points were missing from the 1999 dataset, resulting in 141 values (Table 1). Still other variables, such as distance to MLW bay and to MOSH in 1999, and distance to dune toe, to MLW bay, and to MOSH in 2002, were completely missing from the dataset, and so had no values for that year. We removed variables from the network for years where they were completely missing from the dataset, but we did not omit variables that had occasional gaps from the

List of variables and bin categories included in our Bayesian network linking physical features and site fidelity to piping plover (*Charadrius melodus*) nest presence and absence, using three years of data on nest points and random points without nests from Assateague Island National Seashore, MD, USA.

Variable ^a	Number of real values $(n)^{b}$			Bin categories ^c				
	1999	2002	2008	1	2	3	4	5
Beach width (m)	119	117	140	0-50	50-100	100-150	150-200	200-400
Distance to dune crest (m)	144	122	140	0-100	100-200	200-400	400-600	600-1000
Distance to dune toe (m)	144	0	140	0-100	100-200	200-400	400-600	600-1000
Distance to MHW bay (m)	144	122	140	0-100	100-200	200-300	300-400	400-1000
Distance to MHW ocean (m)	144	122	140	0-100	100-150	150-200	200-300	300-1000
Distance to MLW bay (m)	0	0	140	0-100	100-200	200-300	300-400	400-1000
Distance to MOSH (m)	0	0	140	0-75	75-150	150-225	225-375	n/a
Elevation (m)	144	122	140	-0.5 to 0.5	0.5-1.5	1.5-2.5	2.5-3.5	n/a
Nest attempt	144	122	140	Absent	Present	n/a	n/a	n/a
On foredune	144	122	140	No	Yes	n/a	n/a	n/a
Site fidelity	144	122	140	None	Potential	n/a	n/a	n/a
Slope (%)	144	110	140	0-2.5	2.5-5.0	5-7.5	7.5-50	n/a
Vegetation	144	122	140	Sparse	Herbaceous	n/a	n/a	n/a

^a "Beach width (m)" is the horizontal distance between the dune-toe boundary and the mean low water (MLW) line, "Distance to dune crest (m)" is the perpendicular distance from the dune high boundary to the nest or random point without nest, "Distance to dune toe (m)" is the perpendicular distance from the dune low boundary to the nest or random point without nest, "Distance to MHW bay (m)" is the perpendicular distance from the mean high water bay boundary to the nest or random point without nest, "Distance to MHW ocean (m)" is the perpendicular distance from the mean high water ocean boundary to the nest or random point without nest, "Distance to MLW bay (m)" is the perpendicular distance from the mean high water ocean boundary to the nest or random point without nest, "Distance to MLW bay (m)" is the perpendicular distance from the mean high water ocean boundary to the nest or random point without nest, "Distance to MLW bay (m)" is the perpendicular distance from the mean low water bay boundary to the nest or random point without nest, "Distance to MCSH (m)" is the closest distance from a moist substrate area to the nest or random point without nest, "Elevation (m)" is the vertical height above sea-level of the nest or random point without nest (absent), "On foredune" indicates whether the nest or random point without nest is on (yes) or off (no) a constructed foredune, "Site fidelity" indicates whether a nest or random point without nest is within 75 m (potential) or not (none) of a nest or random point without nest of the nest or random point without nest, "Levation at the nest or random point without nest, "Some point without nest, a 5 m radius of the nest or random point without nest, "Vegetation" is the general type and density of vegetation at the nest or random point without nest.

^b Real values of '0' indicate variables for which no data was available and thus were not included in the network. Variables that have lower real values than the highest real value for that year indicate a certain proportion of data was not available. These variables were still included in the network, because Bayesian networks are designed to accommodate missing data.

^c Bin categories are non-overlapping.

network because BN's are designed to incorporate missing data. Uncertainty is propagated through the network because missing values are explicitly incorporated into the probability distributions that determine the likelihood of the outcome.

2.2. Model development

We first created a diagram, based on previous literature and expert opinion, that illustrated how each of 12 explanatory variables (i.e. physical features of piping plover nesting habitat) interacted and how each explanatory variable influenced the response variable of plover nest presence or absence (Burger, 1987; Cohen, 2005; Cohen et al., 2008, 2009; Houghton, 2005; Maslo et al., 2011; Powell and Cuthbert, 1992). Next, we converted this diagram into a BN using Netica 4.16 (Fig. 4). Each variable in the BN was indicated by a node (box) that represented a set of probabilities that were conditional on the other variables in the network (illustrated by arrows; Fig. 4); the variables that feed into other variables are known as parent nodes and the variables that parent nodes feed into are known as child nodes. The final step in constructing the BN was to calculate conditional probability distributions for each variable in the network; these distributions can be calculated based on scientific literature, expert opinion, or by fitting the network to observed data (Charniak, 1991). We used three years of observed data (1999, 2002, 2008) to calculate the conditional probability distributions for each variable. The set of probabilities for each child node was conditioned on every possible combination of states for its parent nodes. The final constructed Bayesian network graphically represented the joint probability distribution over a set of statistical variables, described mathematically as:

$$P(X_1...X_n) = \prod_i P(X_i \ Pa(X_i))$$

where $P(X_i)$ is the probability of a variable X_i and $Pa(X_i)$ is a parent variable of X_i in a Bayesian network (Koller et al., 2007).

2.3. Assessing model performance

We generated the BN's conditional probability distributions (hereafter "trained") with each year of data (1999, 2002, 2008) and assessed model performance in predicting the response of nest presence or absence for each year and combinations of years. Within individual years, we assessed how well the model performed (hereafter "single year models"). We tested combinations of years by training the model on one year, two years, or all three years of data and assessing how well the model predicted nest presence or absence for one year, two years, or all three years, covering all possible combinations (hereafter "multiple year models"). If data were completely missing for a variable in one year, we removed that variable in multiple year models as well. We used log-likelihood ratios (LR) and error to assess prediction accuracy, and outcome uncertainty (Marcot, 2012) in various model scenarios that were based on single year and multiple year datasets.

LR values indicate the likelihood of a model's prediction for a given observation over the prior likelihood for that observation. The prior probability can be generated based on previous knowledge, data, or can be a prior that is uninformed if insufficient knowledge of data exists. We generated model predictions based on inputs from the existing datasets and a noninformative, uniformly distributed prior (also termed vague, flat, or diffuse; Kéry and Schaub, 2012) for the nest presence/absence variable. To calculate an LR value for a model, the probabilistic prediction is weighed against the corresponding prior probability, described mathematically as:

 $LR_i = \log\{P(O_i)\} - \log\{pprior(O_i)\}$

where LR_i is the likelihood ratio. $p(O_i)$ is the prediction probability for the observation O_i . *pprior*(O_i) is the corresponding prior probability for the observation O_i .

If LR=0, then $\log\{p(O_i)\} = \log\{pprior(O_i)\}$ indicating the prediction is just as likely as the prior and the prediction offers no improvement.



Fig. 4. Bayesian network showing probabilities of piping plover (*Charadrius melodus*) nest presence (50.1%) and absence (49.9%) conditioned on 2008 data from all 12 physical and site fidelity variables from Assateague Island National Seashore, MD, USA; constructed using Netica BN software (Norsys, 1992–2010). The probabilities are similar for nest presence and absence because the data included near equal numbers of nest and random points. Variables for which there was no data in 1999 (i.e. distance to MLW bay and to MOSH) and 2002 (i.e. distance to dune toe, to MLW bay, and to MOSH) were excluded from the network for those years and for combined years including those years, although the structure remained the same as that of 2008. Arrows represent the direction of conditional dependencies among variables, and black bars represent the probabilities for each state, with specific probability values indicated next to the bars. Numbers at the bottom of nodes are mean (i.e. expected value) and standard deviation. For continuous variables, the mean is represented mathematically by the equation $\mu = \int_{-\infty}^{\infty} xp(x) dx$ and for discrete variables with assigned state values, the mean is represented by the equation $\mu = \sum_{x} x p(x)$.

If LR>0, then $\log\{p(O_i)\}$ > $\log\{pprior(O_i)\}$, indicating the prediction is more likely that the prior and the prediction is an improvement.

If LR < 0, then $\log\{p(O_i)\} < \log\{pprior(O_i)\}$, indicating the prediction is less likely than the prior (Weigend and Bhansali, 1994).

Being a hind-casting model, we assessed model prediction accuracy by verifying the extent to which the predictions matched the actual observations of nests and random points for single year and multiple year datasets. We thus generated LR values for various model scenarios (hereafter, 'LR_{predict}') and compared these values to reference LR values for those same models. The reference LR values represented perfect predictions because they were based solely on the actual nest and random point location data for the corresponding model (hereafter, 'LR_{actual}'). In other words, LR_{predict} indicated the likelihood of our model predictions compared to the likelihood of the uninformed priors for those models, whereas LR_{actual} indicated the likelihood of the uninformed priors for those model compared to the likelihood of the uninformed priors for those model that represented the change in the LR_{predict} from the LR_{actual}:

$$percentage change = \frac{LR_{predict} - LR_{actual}}{|LR_{actual}|} \times 100$$

A change of 0 would thus represent a model in which the prediction was just as likely as the actual data (i.e. the prediction is highly accurate because it perfectly matches the actual data). Thus, 0% change would indicate that the response variable (nest presence or absence) depended strongly on the explanatory variables. A negative change would indicate the prediction is less accurate (i.e., the response variables are less dependent on the explanatory variables) than the data. The more negative the difference, the less dependent the response variable is to the explanatory variables. A change of -100% would be produced from an LR_{predict} of 0, thus indicating that the model is no better than the uninformed prior. Positive change would be the actual data.

Error values quantify the proportion of predictions that did not match the actual data; for example, a prediction of nest presence at a location where no nest was observed and vice versa. We explored outcome uncertainty from these errors by analyzing the proportion of true positives, true negatives, false positives, and false negatives in our model predictions. True positives are cases where nest presence predictions matched observed nests, and true negatives are cases where nest absence predictions matched randomly selected observation points where nests were not found. False positives are cases where the model predicted nest presence but in the actual data a nest was not present, and false negatives are cases where the model predicted the absence of a nest but there actually was a nest in the data. Many true positives and few false negatives indicate that the model is able to predict nest presence with a high degree of certainty. Many true negatives and few false positives indicate that the model is able to predict nest absence with a high degree of certainty. All LR and error values were generated using code developed in MATLAB 8.2.

We additionally assessed outcome uncertainty by using Netica's graphical interface to change the probabilities of each variable in our network to reflect conditions that were favorable (highest probability of a nest being present, given a specific range of physical variables) and unfavorable for nesting (highest probability of a nest being absent, given a specific range of physical variables). We analyzed these probabilities in conjunction with visual observations of changes in nest distributions and by using habitat maps to calculate the percent change in sparsely vegetated habitat in 1999, 2002, and 2008.

2.4. Assessing model sensitivity

We assessed model sensitivity to variables in two unique ways (Marcot, 2012). First, within each single year model, we assessed single variable influence by comparing the difference in LR of the model before and after sequentially removing each variable. In this case, the network was trained using all available variables for each year and predictions were generated after each variable was sequentially removed. This method of sensitivity analysis allowed us to compare the sensitivity rankings of variables in our single year models, thus indicating whether the posterior probability distributions for variables in our 1999, 2002, and 2008 single year models differed. Second, we assessed the effect on model performance of removing variables completely from the dataset used to train the model and generate predictions. This method of variable removal is useful to future users of this model who may be limited by data availability and need to have an understanding of the impact of these limitations. Further, the most parsimonious model is desired by researchers as well as managers. In this case, we used our best performing single year and multiple year models to explore variable removal because we wanted to compare the effects on model performance of variable removal across a range of datasets.

To determine a sequence for removing variables in the latter method of assessing model sensitivity, we first tested the effects of removing each variable individually on model performance. Individual variables that did not have any effect on model performance (i.e. no change in LR or error values between the model with the variable removed and the model with all variables included) were removed in combination from the model. Because some of the variables were not available in all years, we additionally removed the variables that were only available in one year. For the remaining variables, we assessed whether any were highly correlated. If not already removed by the steps above, we compared how the removal of each variable from any pair of highly correlated variables (Pearson product-moment correlation coefficient of >0.75 or <-0.75) affected model performance and removed the variable of the pair that was the most difficult, time-consuming, or expensive to obtain. Lastly, as many of the explanatory variables were extracted from lidar data and aerial photography, which are not always available at a site and are expensive to obtain, we additionally removed all explanatory variables that could be obtained solely from lidar and assessed the performance of this very simple model.

2.5. Model applications

We present two examples of how our model's Bayesian network framework can be used to test hypotheses about piping plover nest site selection on barrier islands; the testing approach and results are described in Section 3. We hypothesized that including nests on the foredune would increase model uncertainty because the constructed foredune was an anomalous nesting area for piping plovers due to the fact that it is an elevated feature ('foredune hypothesis' in Section 3). We based this hypothesis on previous literature on piping plover nest site selection, which shows that, in the absence of this feature, plover nest sites would be predominantly located on flat, low elevation bayside sites where plovers would have the best access to low-energy MOSH (Cohen, 2005; Fraser et al., 2005; Houghton, 2005). We used our best overall performing model to test this hypothesis by comparing its performance when trained and predicting for a dataset based only on points that were off the constructed foredune to a dataset based only on points that were on the foredune.

We also hypothesized that we could use our BN to illustrate that shifting distributions of plover nests ('shifting distributions hypothesis' in Section 3) were related to certain habitat changes that occurred from 1999 to 2008. Visual observations of nest distributions in ArcGIS revealed that nests in 2008 appeared to be concentrated closer to the ocean high tide line and dune line, which followed closely the boundary of sparse and herbaceous vegetation compared to 1999 when nests were spread out across the interior of the island, closer to the bayside high tide line, and farther from dunes and the ocean high tide line (Fig. 2). We predicted based on these visual observations that conditions favorable for plover nesting should transition, following foredune construction, from preferred low elevation, low slope, sparsely vegetated areas near bayside MOSH toward the less-preferred ocean-side and closer to the dune line to avoid flooding from high tides. We tested this hypothesis by comparing the physical conditions that produced the highest probabilities of nest presence to the conditions that produced the highest probabilities of nest absence using BNs for each single year model.

3. Results

3.1. Model performance

3.1.1. Single year

In all scenarios, the LR_{predict} values were >0 (Table 2), indicating that the model prediction was more likely than the prior. The percentage change in LR between the actual versus predicted model output (larger differences indicate less certainty) was -65% in 1999, -59% in 2002, and -58% in 2008 (Table 2). Total error (combined false negatives and false positives) was 17% in 1999, 11% in 2002, and 3% in 2008 (Table 2). The percentage of total error due to false negatives (a nest predicted to be absent when it was present in the data) was much lower (17% in 1999, 14% in 2002) than the percentage due to false positives (a nest predicted to be present when it was absent in the data; 83% in 1999, 86% in 2002) in both 1999 and 2002. In 2008, the percentage of the overall 3% error due to false negatives (50%) and false positives (50%) was equal (Table 2).

3.1.2. Multiple year

When we used any one year to train the model, and predicted for a single different year, we found poor model performance (Table 2). While all of the LR_{predict} scores were again positive, we found that the percentage change in LR was -97% when we trained our model with 1999 data and asked it to predict nest probability for 2002 and -98% using 2008 data to predict nest probability for 1999. Error ranged from 43 to 47% for all these cross-year models. The percentage of the error that was due to false negatives (a nest predicted to be absent when it was present in the data; 0-9%) was again lower than the percentage of the error that was due to false positives (a nest predicted to be there but was absent in the data; 91-100%; Table 2).

We found improved model performance when we used all three years of data to train the model as compared to using a single year to predict a different year; the percentage change between LR_{actual} and

Model performance metrics indicating accuracy and outcome uncertainty of our Bayesian network that links physical features and site fidelity to piping plover (*Charadrius melodus*) nest presence and absence, for single year and multiple year dataset combinations based on three years of data from Assateague Island National Seashore, MD, USA.

Model ^a	Error (%) ^b			Likelihood ratio (LR) ^c		
	Total	False positives	False negatives	LR _{actual}	LR _{predict}	LR change (%)
D1999_P1999	17	83	17	43	15	-65
D2002_P2002	11	86	14	37	15	-60
D2008_P2008	3	50	50	42	18	-58
D1999_P2002	47	91	9	37	1	-97
D1999_P2008	47	100	0	42	0.6	-99
D2002_P1999	45	92	8	43	1	-98
D2002_P2008	45	98	2	42	0.9	-98
D2008_P1999	46	99	1	43	0.8	-98
D2008_P2002	43	96	4	37	1	-97
Dallyrs_P1999	20	72	28	43	15	-66
Dallyrs_P2002	11	85	15	37	15	-60
Dallyrs_P2008	5	72	28	42	18	-56
Dallyrs_Pallyrs	11	74	26	122	48	-60

^a "D" indicates the year of data used to generate the conditional probabilities for the model, "P" indicates the year from which model probabilities were derived from. ^b Total error is the percentage of the model predictions that did not match the data. False positives indicate the percentage of that total error that was attributed the model predicting a nest being present when there was no actual nest observed. False negatives indicate the percentage of that total error that was attributed to the model predicting no nest being present when there actually was a nest observed. The percent false negatives plus the percent false positives equals 100% of total error.

^c LR_{actual} represents the likelihood of the actual data, compared to the likelihood of the prior; LR_{predict} represents the likelihood of the model predictions given the data, compared to the likelihood of the prior; LR change represents the percent change in the likelihood of the actual observed data and the likelihood of the model predictions given the data. Positive LR_{predict} values indicate that the prediction is more likely than the prior. Negative LR change (%) values indicate the prediction is less likely than the data, with smaller negative values indicating that the likelihood of the prediction over the data is improved, in other words the predictions closely matched the actual observed data.

LR_{predict} was improved and error was lower (5-20%; Table 2). Again, most of the total error was explained by false positives (72-85%; Table 2). Training the model on all three years and predicting for all three years again improved over any single cross-year prediction, with a percentage change in LR of -60% and an overall error of 11%, with the majority of that error (74%) again due to false positives (Table 2).

3.2. Model sensitivity

Within each single year model, when we assessed individual variable influence by comparing the difference in LR of the model before and after sequentially removing each variable from models that were trained on all variables, we found sensitivity rankings differed among all years. Site fidelity and beach slope were the only variables that had similar sensitivity rankings across the single year models. Site fidelity was the second most influential variable in 2008 and 2002, and the third most influential variable in 1999. Beach slope was the fifth most influential variable in 2008 and 1999, and the sixth most influential variable in 2002. The most influential variable was beach width in 2008, distance to MHW bay in 2002, and distance to MHW bay in 1999. The differences in the sensitivity rankings among the most influential variables within each year were very small (Fig. 5). For example, the difference between the first and second ranked variable was 1% in 2008, 2% in 2002, and 1% in 1999.

When we assessed the effect on model performance of removing variables completely from the dataset used to train the model and generate predictions in our best performing single year model (D2008_P2008), we found no difference between the performance (LR and error values) of the model with all variables included and the model with the on foredune variable removed, as well as the model with distance to dune toe removed. When we removed these two variables in combination, we found the same error (3%) as for the model with all variables included (Table 3). Distances to MLW bay and to MOSH were only available in 2008; we found the error increased to 4% when we removed these variables from the model, in addition to removing on foredune and distance to dune toe. Distance to MHW ocean and distance to dune crest was the only remaining highly correlated pair after on foredune, distance to dune toe, distance to MLW bay and distance to MOSH had already been removed in the steps above. We removed distance to dune crest from the model because it was more difficult to obtain a complete dataset for this variable than it was for MHW ocean; this removal in addition to removing on foredune, distance to dune toe, distance to MLW bay, and distance to MOSH, did not affect model performance (Table 3). When we explored removing any remaining variables not available through manual field collection (i.e., beach width), in addition to the variables already removed in the steps above, we found reduced model performance, with an error of 9% (Table 3). For this reduced model (that included only four variables; distance to MHW ocean, elevation, slope, and vegetation), a majority of the 9% overall error was again due to false positives (63% of the total error).

When we explored the same sequence of variable removal for our best performing multiple year model (Dallyrs_P2008), we found similar patterns of high percentages of false positives and low



Fig. 5. Likelihood ratio difference (%) for 12 piping plover (*Charadrius melodus*) nest presence variables in 1999, 2002, and 2008 at Assateague Island National Seashore, MD, USA. Likelihood ratio difference represents the difference from the likelihood of the model predictions given data from all 12 variables to the likelihood of the model predictions after removing each variable. In this case, each single year network was trained using all available variables for each year and predictions were generated after each variable was sequentially removed. The larger the likelihood ratio difference, the more influential the variable is to nest presence/absence probability. Dist. means distance.

Model performance metrics of accuracy and outcome uncertainty for our Bayesian network that links physical features and site fidelity to piping plover (*Charadrius melodus*) nest presence and absence, for combinations of variables removed from the datasets derived from Assateague Island National Seashore, MD, USA. In this case, we analyzed model sensitivity by assessing the effect on model performance of removing variables completely from the dataset used to train the model and generate predictions; using first our best overall performing model trained on 2008 and predicting based on 2008 (D2008_P2008) and second our best performing model trained on multiple years and predicting based on 2008 (Dallyrs_P2008).

Variable (s) removed ^a	Error (%) ^b		LR difference from full model (%) ^c	
	Total	False positives	False negatives	
D2008_P2008 model				
None	3	50	50	0
Beach width	4	60	40	-0.7
Distance to dune crest	3	50	50	-0.2
Distance to dune toe	3	50	50	0
Distance to MHW bay	4	100	0	0.4
Distance to MLW bay	3	50	50	-0.2
Distance to MHW ocean	3	50	50	-0.3
Distance to MOSH	4	60	40	-2
Elevation	4	67	33	2
On foredune	3	50	50	0
Site fidelity	4	40	60	1
Slope	4	100	0	-0.3
Vegetation	3	50	50	-0.6
FD, DT	3	50	50	0
FD, DT, MLWB, MOSH	4	67	33	-0.8
FD, DT, MLWB, MOSH, DC	4	67	33	-0.8
FD, DT, MLWB, MOSH, MHWO	6	63	37	-0.5
FD, DT, MLWB, MOSH, DC, MHWB, BW, SF	9	63	37	-3
Dallyrs_P2008 model				
FD, DT, MLWB, MOSH	5	72	28	-0.5
FD, DT, MLWB, MOSH, DC	4	67	33	-0.3
FD, DT, MLWB, MOSH, DC, MHWB, BW, SF	26	73	27	-20

^a "Beach width (m)" (BW) is the horizontal distance between the dune-toe boundary and the mean low water (MLW) line, "Distance to dune crest (m)" (DC) is the perpendicular distance from the dune high boundary to the nest or random point without nest, "Distance to dune toe (m)" (DT) is the perpendicular distance from the dune low boundary to the nest or random point without nest, "Distance to MHW bay (m)" (MHWB) is the perpendicular distance from the mean high water bay boundary to the nest or random point without nest, "Distance to MHW ocean (m)" (MHWO) is the perpendicular distance from the mean high water ocean boundary to the nest or random point without nest, "Distance to MLW bay (m)" (MLWB) is the perpendicular distance from the mean high water ocean boundary to the nest or random point without nest, "Distance to MLW bay (m)" (MLWB) is the perpendicular distance from the mean low water bay boundary to the nest or random point without nest, "Distance to MSH (m)" (MSH) is the closest distance from a moist substrate area to the nest or random point without nest, "Elevation (m)" is the vertical height above sea-level of the nest or random point without nest, "Nest attempt" indicates a nest (present) or random point without nest (absent), "On foredune" (FD) indicates whether the nest or random point without nest is on (yes) or off (no) a constructed foredune, "Sile fidelity" (SF) indicates whether a nest or random point without nest is within 75 m (potential) or not (none) of a nest or random point without nest from the preceding year, "Slope (%)" is the average rise over run within a 5 m radius of the nest or random point without nest.

^b Total error is the total number of model predictions that did not match the data. False positives indicate the percent of total error that was attributed to the model predicting a nest being present when there was no actual nest observed. False negatives indicate the percent of total error that was attributed to the model predicting no nest being present when there actually was a nest observed.

^c LR difference from full model (%) is the percent difference between the Likelihood Ratio (LR) of the full model with all variables included and the LR of the model with variable(s) removed.

percentages of false negatives despite increases in overall errors. The reduced model trained on all years (that included only the four variables of distance to MHW ocean, elevation, slope, and vegetation) had an error of 26%, with most of that error (73%) attributable to false positives (Table 3).

3.3. Model applications

3.3.1. Constructed foredune hypothesis

We hypothesized that including nests on the foredune would increase model uncertainty because the constructed foredune was an anomalous nesting area for piping plovers due to the fact that it is an elevated feature. The average elevation of nests on the constructed foredune in 1999, 2002, and 2008 was higher $(1.8 \pm 0.2 \text{ m})$; mean \pm SE) than the average elevation of nests in the rest of the study area $(1.0\pm0.4 \text{ m})$ in those years. The percentage of total area on and around the foredune (defined as the area east and west of the foredune, and including the foredune itself) that was composed of sparsely vegetated habitat was 87% in 1999; as vegetation encroached the area, the extent of sparsely vegetated habitat then decreased to 64% in 2002, and to 43% in 2008. By contrast, the percentage of total area off and away from the foredune that was composed of sparsely vegetated habitat was 45% in 1999, it decreased to 37% in 2002, but then increased slightly to 38% in 2008. The percentage of total nests in our study area that were located on the foredune increased from 1998 (5%) to 2002 (19%) and again dramatically in 2008 (47%). When we included only the nest and random points that were off the foredune in our BN trained with the 2008 data, we found 0% error in comparison to the model that included all nest and random points which had an error of 3% (see D2008_P2008, Table 2). Conversely, when we included only the points on the foredune, we found a much higher error (10%) compared to the model that included all of our data points (see D2008_P2008, Table 2).

3.3.2. Shifting distributions hypothesis

We hypothesized that we could use our BN to illustrate that shifting distributions of plover nests were related to certain habitat changes that occurred from 1999 to 2008. We found that the ranges of conditions favorable versus unfavorable for nesting differed more in 2008 than in 2002 and 1999 (Table 4). The ranges of conditions for just one variable (site fidelity) were different for the most favorable (80% probability of a nest being present) and unfavorable (75% probability of a nest being absent) nesting conditions in 1999 (Table 4). In 2002, the ranges of conditions for all but three variables (distance to dune crest, distance to mean high water ocean, and on foredune) were different for the most favorable (86% probability of a nest being present) and unfavorable (80% probability of a nest being absent) nesting conditions (Table 4). Finally, in 2008 ranges of conditions for all variables, except slope, were

Environmental conditions favorable and unfavorable for piping plover (Charadrius melodus) nesting, derived from our Bayesian network developed using three years of data from Assateague Island National Seashore, MD, USA.

Variable ^a	1999		2002		2008	
	Favorable ^b	Unfavorable	Favorable	Unfavorable	Favorable	Unfavorable
Beach width (m)	50-100	50-100	50-100	0–50	100-150	0-50
Distance to dune crest (m)	200-400	200-400	200-400	200-400	0-100	200-400
Distance to dune toe (m)	200-400	200-400	n/a	n/a	0-100	200-400
Distance to MHW bay (m)	0-100	0-100	100-200	0-100	300-400	0-100
Distance to MLW bay (m)	n/a	n/a	n/a	n/a	300-400	0-100
Distance to MHW ocean (m)	300-1000	300-1000	300-1000	300-1000	100-150	300-1000
Distance to MOSH (m)	n/a	n/a	n/a	n/a	150-225	0-75
Elevation (m)	-0.5 to 0.5	-0.5-0.5	0.5-1.5	-0.5-0.5	1.5-2.5	-0.5-0.5
Nest site fidelity	Yes	No	Yes	No	Yes	No
On foredune	No	No	No	No	Yes	No
Slope (%)	0-2.5	0-2.5	0-2.5	2.5-5.0	2.5-5.0	2.5-5.0
Vegetation ^c	Sparse	Sparse	Shell bed	Herbaceous	Sparse	Herbaceous

^a "Beach width (m)" is the horizontal distance between the dune-toe boundary and the mean low water (MLW) line, "Distance to dune crest (m)" is the perpendicular distance from the dune high boundary to the nest or random point without nest, "Distance to dune toe (m)" is the perpendicular distance from the dune low boundary to the nest or random point without nest, "Distance to MHW ocean (m)" is the perpendicular distance from the mean high water ocean boundary to the nest or random point without nest, "Distance to MHW ocean (m)" is the perpendicular distance from the mean high water ocean boundary to the nest or random point without nest, "Distance to MLW bay (m)" is the perpendicular distance from the mean high water ocean boundary to the nest or random point without nest, "Distance to MLW bay (m)" is the perpendicular distance from the mean high water ocean boundary to the nest or random point without nest, "Distance to MLW bay (m)" is the perpendicular distance from the mean high water ocean boundary to the nest or random point without nest, "Distance to MLW bay (m)" is the perpendicular distance from the mean low water bay boundary to the nest or random point without nest, "Distance to MLSH bay (m)" is the closest distance from a moist substrate area to the nest or random point without nest, "Elevation (m)" is the vertical height above sea-level of the nest or random point without nest, "Nest attempt" indicates a nest (present) or random point without nest (absent), "On foredune" indicates whether the nest or random point without nest is on (yes) or off (no) a constructed foredune, "Site fidelity" indicates whether a nest or random point without nest, is within 75 m (potential) or not (none) of a nest or random point without nest for vegetation at the nest or random point without nest.

^b "Favorable" corresponds to a nest presence probability of 80% in 1999, 86% in 2002, and 80% in 2008. "Unfavorable" corresponds to a nest absence probability of 75% in 1999. 80% in 2002, and 75% in 2008.

^c "Shell bed" is a type of sparsely vegetated habitat present only in 2002, resulting from severe storms in 2001 that deposited large amounts of shell in plover nesting areas.

different for the most favorable (80% probability of a nest being present) and unfavorable (75% probability of a nest being absent) nesting conditions (Table 4).

As the physical habitat became more variable between 1999 and 2008, our BN captured the connection between the shift in distribution of nests that we visually observed and this habitat change as we found that the highest probability of nest presence in 2008 corresponded to habitat that was more sloped (2.5–5.0% in 2008 vs. 0–2.5% in 1999 and 2002), higher in elevation (1.5–2.5 m in 2008 vs. –0.5 to 1.5 m in 1999 and 2002), on wider beach widths (100–150 m in 2008 vs. 50–100 m in 1999 and 2002), closer to the ocean (100–150 m in 2008 vs. 300–1000 m in 1999 and 2002), closer to the dune lines (0–100 m in 2008 vs. 200–400 m in 1999 and 2008), and farther away from the bayside high tide line (300–400 m in 2008 vs. 0–100 m in 1999 and 100–200 m in 2002) as compared to 1999 and 2002 (Table 4).

4. Discussion

Using a Bayesian network constructed with expert knowledge from peer-reviewed literature and trained with historical data, we were able to accurately predict nest presence on ASIS for a historical dataset of nest locations from 1999, 2002, and 2008. Our findings demonstrate that piping plover nest presence can be predicted using a Bayesian network that is primarily based on physical features of barrier island habitats.

Our BN illustrated, as expected based on past field work (e.g., Cohen et al., 2009), that in the post-storm environment of 1999, the ranges of physical conditions were very similar for favorable and unfavorable nesting conditions on the North End of ASIS. Field studies have repeatedly shown that piping plovers typically nest on flat, low-lying beaches with clumped sparse vegetation near MOSH, as is often found in areas of storm-created overwash (Cohen, 2005; Cohen et al., 2008, 2009; Fraser et al., 2005; Houghton, 2005). The 1998 storms created these conditions across much of the North End. Our model based on 1999 nesting data performed poorly in distinguishing between nest sites and random sites without nests in 1999, likely because the habitat was uniformly of high quality

for piping plovers. We saw this lack of poor quality nesting habitat in 1999 reflected in the details of the error. Specifically, we found that our overall error was composed of a much higher percentage of false positives (a nest predicted to be present when it was absent in the data) than false negatives (a nest predicted to be absent when it was present in the data) which we would expect if the majority of the habitat is suitable for nesting yet demographic factors such as population size and inter- and intra-specific competition prevent plovers from occupying every available, suitable nesting site. Detailed examination of the explanatory variable ranges for the false positives revealed no single explanatory variable was a likely driver of false positives. Considering that the priority of this model is to accurately predict nest presence, and given that demographic factors likely prevent piping plovers from occupying every potential nest site, we would be concerned about our model's ability to accurately predict nest presence if there were many false negatives because this result would indicate that the model is not able to recognize physical conditions that are most suitable for plover nesting. For all our models that did not distinguish well between nests and random sites, the majority of the error was due to false positives, even for those models with much higher error rates than our best performing model. For those cases where the model output was a false negative, we discovered that the model prediction itself was near equivocal. For example, for the D2008_P2008 model, there were two false negatives, where the model predicted a nest to be absent when it actually was present in the data. For both of those cases, the model predicted probability of nest absence was 0.6.

The shifting distribution of nests from 1999 to 2008 (see Fig. 2) suggests that the physical changes in beach morphology and vegetation, due to both the construction of the foredune (Schupp et al., 2013) and related lack of storm-related overwash, led the North End of ASIS to transition from more physically uniform habitats in 1999 to a more varied habitat in 2008. As vegetation structure shifted from predominantly sparse to more herbaceous and shrub communities near preferred foraging areas of bayside MOSH, piping plover nest locations moved toward the ocean-side of the North End. Our model performed better at predicting both nest presence and nest absence under the more varied habitat conditions in 2002 and best in 2008 (with an error of only 3%) when there was a more even proportion of suitable and unsuitable habitat than in 1999. The few misclassifications in our best-performing model of 2008 nesting conditions were spread equally among false positives and false negatives, suggesting that the model was able to learn which physical conditions presented both unfavorable and favorable nesting habitat when the habitat was highly varied. From discussions with wildlife managers on the issue of predicting sea-level rise and human development effects to shorebird nesting habitat, we expect that future applications of this model will be at a much coarser spatial scale (i.e., 1 km²) than was used in this initial model development (i.e. points of nests or random points with an error of 1–5 m). We expect that as spatial scale increases, habitat heterogeneity will increase as well and our current model will do well at predicting future piping plover locations in a heterogeneous barrier island environment.

We think that differences in morphological conditions present in 1999, 2002, and 2008 negatively affected the model's cross-year predictive capability. The transition in physical island features from 1999 to 2002-2008 resulted in poor predictive capabilities when a model based on one year of data was used to predict nest and random points of another year alone. However, when the model was based on all three years of available data, nest and random point predictions were more accurate for 2002 alone, 2008 alone, or for all three years combined than when based on a single different year. Further, we found little similarity in model sensitivity to single explanatory variables for each year, indicating that habitat differences among 1999, 2002, and 2008 were pronounced enough to result in different posterior probability distributions for the variables in each year's model. In applications of this model to predict future probabilities of piping plover nest presence on the North End of ASIS or at other sites, the use of all three years of data in the model are preferred, as it is not possible a priori to know whether future habitat conditions will most closely resemble the uniformly high quality habitats of 1999 or varied habitats of 2008. Using all three years of habitat data allows future predictions to be based on a BN parameterized with a fuller range of habitat quality for nesting piping plovers. And, perhaps, the three years that were used are fully representative of the relevant physical conditions needed for making good predictions. If additional years of piping plover and habitat features becomes available, these data can be included in future predictions from the BN model trained on as wide of a base of available data as possible.

In addition, we suggest the use of a BN without the on foredune and distance to dune toe variables in future applications, as removal of these two variables created a simpler model without increasing error or decreasing predictive capabilities. The constructed foredune was a preferred nesting site even though it was elevated in height and far from bayside MOSH. We discovered the BN that included only nest and random points that were off the foredune performed better than the model that included only the points that were on the foredune and the original model with points on and off the foredune; these results supported our expectation that at least some of the error and uncertainty present in our 2008 model was driven by the foredune constructed on the North End. Further, we found that the highest probability of nest presence in our BN that was based on 2008 data corresponded to habitat that was more sloped, higher in elevation, closer to the ocean, and farther away from the bayside high tide line as compared to the BN's based on 1999 and 2002 data, contrasting with our original predictions that plovers would continually nest on low elevation flat bayside sites that would provide them with the best access to low-energy MOSH. Thus, the BN model was able to predict how physical conditions favorable for nesting shifted with the shifting availability of physical habitats driven by lack of island overwash and vegetation encroachment related to the constructed foredune. Other studies have demonstrated that site fidelity exerts a strong influence on piping plover nest site selection (Cohen et al., 2006), and we also found that site fidelity (i.e., proximity to prior year's nest sites) was one of the most influential variables in our models (Fig. 5). We expect that site fidelity alone may partly explain why piping plovers in our study area continued to nest in the same general location even after the foredune was constructed and habitat conditions changed dramatically.

Including metrics related to the proximity of nests to the bayside MLW and MHW tidelines, and MOSH resources, as variables in the model when data availability permits is desirable, as field studies have consistently shown the importance of those resources to piping plover nest site selection (Cohen, 2005; Loegering and Fraser, 1995). However, when data are available for only a small portion of the 12 variables we included in the model, we are confident that it is still able to reliably predict plover nest presence as was shown in the low rates of false negatives for our reduced model that included only the four variables of distance to MHW ocean, slope, elevation, and vegetation.

5. Conclusions

This study represents an important step toward predicting future changes to piping plover nesting habitat related to sealevel rise and human development. We have presented a modeling method that predicts the probability of plover nest presence and absence primarily using physical features and based on a varied historical dataset that can be adapted to different areas. With this initial model, we were able to reliably predict the presence of nests based on a dataset with a wide range of physical conditions using a Bayesian network that linked physical variables and a metric of site fidelity to nest and random points, and we were able to identify how habitat variation affected the model's performance. Given the importance of site fidelity found in our model, and the important influence of vegetation encroachment on the physical features selected by nesting piping plovers, opportunities exist to explore beach management practices that (1) reduce disturbance to nesting habitats that might prevent plovers from establishing nests at sites previously used and (2) encourage processes such as overwash that prevent vegetation encroachment.

This model, based on all three years of data and thus encompassing uniform to highly varied physical habitats, may be used to predict future probabilities of nest presence under varied scenarios where the physical environment is altered by human development, storms and sea-level rise. As a future application, this model could be coupled to a barrier island geomorphology model to predict how large scale shoreline change rates caused by sea-level rise will affect plover nest presence at other locations beyond the North End of ASIS. If data are incomplete for such a future application of this model, a simpler model based on 1999, 2002, and 2008 could be used, with on foredune, distance to dune toe, to MLW bay, and to MOSH removed. In the absence of lidar elevation data or aerial photography, then a very simple model trained on the same years, and including only the following variables: distance to MHW ocean, elevation, slope, and vegetation, may be used.

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Quantifying the cascading effects of sea-level rise and management decisions on barrier island shoreline change, geomorphology, and nesting habitat of the federally-threatened Piping Plover (*Charadrius melodus*)

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Abstract

Barrier island habitats provide essential ecosystem services for human populations and support a number of imperiled wildlife species. These island habitats are susceptible to the effects of sealevel rise and storms, particularly because they are exposed to the open ocean and are low in elevation. Additionally, many barrier islands have been modified by humans such that the natural responses of these islands to sea-level rise and storm surge have changed. Given that sea-level rise rates are projected to increase over the next century, and the importance of barrier islands for both humans and wildlife, there is an urgent need to predict how sea-level rise will affect these islands in the future. We present three linked Bayesian Networks (BNs) that serve as probabilistic models to forecast sea-level rise effects on barrier island habitats by linking the effects of (1) sea-level rise and shoreline change to (2) subsequent dynamic change in geomorphological features, including the effects of potential beach nourishment actions, and finally to (3) changes in the probability of nest presence for the federally-listed Piping Plover (Charadrius melodus), a beach-dependent shorebird. Using datasets for Assateague Island in Maryland and Virginia in 1999, 2002, and 2008, we developed and tested the linked BNs to evaluate the changes in the probability Piping Plover nesting suitability. In developing the BNs,

we compared predicted and actual nest locations for these years. We forecasted the effects of various combinations of sea-level rise rates and beach nourishment strategies on a portion of the island for which data used to inform the model were most complete. Our findings indicate that modest sea-level rise rates may yield more Piping Plover nesting habitat at this location in the future but that certain beach nourishment strategies may reduce this increase in nesting habitat by encouraging vegetation growth that would decrease suitable habitat. This linked model is broadly applicable to other barrier island settings in the U.S. and elsewhere.

Introduction

Barrier islands are prominent features along the U.S. coastline, spanning 3700 km and covering an area of 6800 km² along the Atlantic and Gulf Coasts (Zhang and Leatherman 2011). These elongated, predominantly sandy islands and their associated bayside marshes provide a myriad of regulating and supporting (e.g., nutrient retention and cycling, storm surge protection, mainland shoreline stabilization), provisioning (e.g., nurseries for recreational and commercial fish, waterfowl populations) and cultural (e.g., beach recreation, fishing, hunting) services for human populations (Hassan et al. 2005, White et al. 2010, Barbier 2012). These ecosystem services originate from a variety of barrier island habitats, including coastal forests, dunes, tidal marshes, salt flats, and sandy beaches that also provide habitat for many wildlife species. Further, a number of rare species, including American Oystercatchers (*Haematopus palliatus*), Wilson's Plovers (Charadrius wilsonia), Least Terns (Sternula antillarum), Common Terns (Sterna hirundo), Gull-billed Terns (Gelochelidon nilotica), Black Skimmers (Rynchops niger), Piping Plovers (Charadrius melodus), Northeastern beach tiger beetles (Cicindela dorsalis dorsalis), Loggerhead (Caretta caretta) and Green (Chelonia mydas) sea turtles, and Seabeach Amaranth (Amaranthus pumilus) depend on these barrier island habitats (U.S. Fish and Wildlife

Service 1996). Management of these imperiled species takes place in the context of management for the totality of ecosystem services noted above and in the context of continued access to beaches for recreation as well as modification related to storm protection (Schlacher et al. 2007, Weinstein et al. 2007, White et al. 2010, Aretxabaleta et al. 2014).

Approximately 22.4 million people live in U.S. census blocks that border the open ocean coast or that are directly subjected to coastal flood hazards (Crowell et al. 2010). Furthermore, approximately 1.4 million people live on barrier islands along the U.S. Atlantic and Gulf Coasts, and this population has been increasing steadily in all but two of the 18 states where barrier islands occur (Zhang and Leatherman 2011). Given the popularity of barrier islands for recreation and associated development, as well as the wide array of ecosystem services accessed by people living near the coast or simply visiting these island habitats, managers are required to consider efforts to modify barrier islands to achieve varied ecosystem service goals. Human modification of barrier island habitats is challenging as barrier islands are, by their nature, continually reshaped by wind, waves, currents, tides, and bio-physical feedbacks with marsh and terrestrial vegetation. The position of these islands between the open ocean and the mainland, coupled with their generally low elevation, make them especially vulnerable to, yet by their nature morphologically-responsive to, the effects of storms (Morton and Sallenger 2003, Stockdon et al. 2009, Doran et al. 2012) and sea-level rise (SLR; Williams 2013). This vulnerability to SLR, coupled with management practices that often focus on flood prevention and returning the barrier islands to pre-storm morphological states, can impair ecosystem services provided by barrier islands, which has enormous potential consequences for wildlife and human populations.

A recent projection estimates that the mean global mean sea level for the years 2046-2065 will range from 0.24–0.29 m higher than that for the years 1986–2006, with a predicted increase to 0.43–0.73 m by the year 2100 (Intergovernmental Panel on Climate Change 2013). However, forecasting how SLR will alter barrier islands over the 21st century is difficult due to varying effects across islands, where one barrier island may respond differently from another to the same SLR rate due to differences in the morphological composition (Nicholls 2010). Relative SLR incorporates regional variations stemming from ocean circulation patterns, interannual variability (Zhang and Church 2012, Ganachaud et al. 2013), glacial isostatic rebound, and tectonic movements as well as local variations stemming from land subsidence, underwater geomorphology, sediment supply, and subsurface resource extraction (Intergovernmental Panel on Climate Change 2013). For example, barrier islands along the U.S. Mid-Atlantic Coast that have small tidal ranges, large waves, low elevation and slope, and historically high rates of SLR are highly vulnerable (Thieler and Hammar-Klose 1999). Changes in sea level will affect vulnerable areas by inundating them over time, or by driving morphological changes as higher water levels enable wave and tidal driven currents to reshape the coastal landscape. These processes may cause beach erosion and land loss, and changes to other low-lying habitats (Climate Change Science Program 2009, Intergovernmental Panel on Climate Change 2013, Melillo et al. 2014). Therefore, reasonable predictions of the potential impacts of SLR, which are necessary for policy-making, must consider these future changes.

While the effects of SLR alone are projected to be significant, the interactions between SLR and storms, the frequency and intensity of which may be altered with climate change (Intergovernmental Panel on Climate Change 2013), could also be particularly influential for barrier islands. Extreme storm water levels resulting from the combination of tides, storm surge,

and SLR in areas experiencing relatively high SLR have been shown to have an immediate and drastic effect on barrier islands by opening inlets, restructuring dune habitats, and inundating large areas (Colberg and McInnes 2012). Although these are natural processes of these dynamic landforms, predicting these changes remains extremely challenging. Furthermore, storm patterns are generally unpredictable, making predictions related to storm/SLR interactions on barrier islands along the Mid-Atlantic Coast especially challenging (Intergovernmental Panel on Climate Change 2013). A vast majority of the barrier islands along the U.S. Atlantic Coast that are highly valued as areas of development and recreation have been significantly altered by beach stabilization strategies in response to storm risks (U.S. Fish and Wildlife Service 2012). Stabilization strategies include sea walls, groins, and beach nourishment. Beach nourishment actions range from off-shore, near-shore, and on-shore sand deposition to construction of artificial sand dunes, all of which intended to protect and maintain existing anthropogenic infrastructure from storms (Nordstrom 2000, Psuty and Ofiara 2002). Human migration, industrialization and urbanization of coastal barrier islands continues to increase along U.S. coasts and worldwide (McGranahan et al. 2007, Seto 2011, Smith 2011), despite our realization of the risks posed by SLR and storms to these areas. This increasing development pressure is therefore an inherent component in the challenge of understanding how coasts will change in the future and how to adapt to those changes.

Knowledge of the relative future value of particular barrier islands for ecosystem services in general, and wildlife habitat in particular, will help inform decisions related to SLR and storm threats. Here, we have developed a novel system of three linked models, using Bayesian Networks (BNs) to integrate processes functioning on different spatial and temporal scales. BNs are an appropriate modeling framework because their explicit graphical representation conveys

the conceptual framework and they are flexible to allow combinations of continuous physical variables as well as categorical ecological classifications. BNs' incorporation of uncertainty make them ideally suited to investigating the dynamic changes to barrier islands resulting from SLR and for exploring a variety of future scenarios (Pearl 1988, Uusitalo 2007, Koller and Friedman 2009). Our first BN, hereafter the 'shoreline change BN,' links relative SLR rates and extreme storm-induced sea levels to barrier island geomorphology to predict rates of shoreline change at a coarse spatial scale (i.e., 5-km; Gutierrez et al. 2011). Our second BN, hereafter the 'geomorphology BN,' combines the shoreline change predictions (output from the first model) with 11 barrier island geomorphological features and optional beach management parameters (i.e., beach nourishment or foredune construction) to predict morphological characteristics of barrier islands at a finer resolution (i.e., 5-m²; Gutierrez et al. In Review). Our third BN, hereafter the 'plover nest selection BN,' uses the predictions of the geomorphology BN to predict the changes to wildlife habitat, in particular the presence or absence of Piping Plover (*Charadrius melodus*) nests (Gieder et al. 2014).

The Piping Plover, which was federally-listed in 1986 as threatened along the U.S. Atlantic Coast under the U.S. Endangered Species Act (U.S. Fish and Wildlife Service 1985), was chosen as a focal species for this study because individuals nest in sparsely-vegetated, low elevation areas on barrier islands most vulnerable to SLR and storms, and thus are an excellent model species for understanding how these forces will change barrier island wildlife habitat (Wilcox 1959, Kumer 2004, Houghton 2005, Cohen et al. 2009, Schupp et al. 2013). The North Atlantic Landscape Conservation Cooperative has designated the Piping Plover as a representative species on the North Atlantic coast, standing as a surrogate for other species using dynamic beach systems including American Oystercatchers, Least Terns, Black Skimmers, Seabeach Amaranth and migrating shorebirds (U.S. Fish and Wildlife Service 2014). Previous studies have investigated the effects of SLR on wildlife species, including Piping Plovers and Snowy Plovers (*Charadrius nivosus*), but did not explicitly link these effects to dynamic barrier island response. The models used in these prior studies either assumed an average historic SLR rate or static geomorphology, or assumed both these factors together (Seavey et al. 2011, Chu-Agor et al. 2012, Benscoter et al. 2013, Reece et al. 2013a,b, Sims et al. 2013, Gieder et al. 2014).

In this paper, we demonstrate the ability to link three BNs to predict future effects of relative SLR rates and beach nourishment strategies on dynamic shoreline change, island geomorphology and Piping Plover nesting habitat. The BNs were developed and tested separately to determine if each was suitable for developing techniques that could use existing datasets to model future coastal evolution driven by SLR, and Piping Plover response to that coastal evolution (Gutierrez et al., 2011; Gutierrez, In review; Gieder et al., 2014). We evaluated the linked BNs by first hindcasting the probability of plover nest presence on a portion of Assateague Island National Seashore (ASIS) on Assateague Island in Maryland, where the Piping Plover nest selection BN (Gieder et al., 2014) was originally developed, and then hindcasting across all of Assateague Island in Maryland and Virginia, including other areas used and unused by nesting Piping Plovers. We then used the linked BNs to test how various future SLR rates and beach nourishment strategies will likely affect Piping Plover nesting habitat at ASIS in the next 50-100 years.

Methods

Study Site

The study area was Assateague Island, a 58-km barrier island off the coasts of

Maryland and Virginia, U.S. (Figure 1). The U.S. Fish and Wildlife Service's Chincoteague National Wildlife Refuge (CNWR) manages wildlife and public use of wildlife-oriented activities within the Virginia portion and the National Park Service (NPS) manages most of the Maryland portion as ASIS, except for a small portion managed by the state of Maryland as Assateague State Park. Assateague Island supports a variety of habitats including tidal marsh and mudflats on the bayside, coniferous and deciduous forest in the interior, and dunes and sandy beach on the ocean-side. Assateague Island has low elevations with a mean cross-shore elevation of approximately 4 m above mean sea level (all elevations in this study referenced to North American Vertical Datum 1988, NAVD88—mean sea level corresponds to an elevation of 0.34 m in the NAVD88 datum at this location) and widths ranging approximately 220–4500 m.

Bayesian Network Models

We used Netica 4.16 to construct separate Bayesian network models (BNs) that calculated probabilities of barrier island 1) shoreline change (Gutierrez et al., 2011), 2) geomorphologic characteristics (Gutierrez et al., in review) and 3) Piping Plover nest selection (Gieder et al., 2014; Figure 2). In this study, we linked these BNs to the input data and to each other using MATLAB 8.2 so that we could estimate the probability of shoreline change for the entirety of Assateague Island; constrain results for specific SLR rates, and, in turn, use this outcome to constrain the geomorphology BN to estimate the probability of specific barrier island characteristics for that SLR rate. The probability of morphology characteristics was then used as input to constrain the third BN, the plover nest selection BN, to examine the probability for Piping Plover nest presence under past and future conditions. Probabilities for these BNs were derived using point data at coarse (5-km) to

fine scales (5 m) described in further detail below.

Shoreline change BN

The shoreline change BN consists of five variables (Figure 2, Table 1a) that can be used to estimate the probability of future shoreline changes based on historical observations from the U.S. Atlantic coast. Shoreline change rate is the extent, in m/yr, by which the shoreline location changes in time and is based on data derived from different reference features, measurements, and rate-of-change calculations obtained using published reports, historical shoreline change maps, field surveys and aerial photographs. The shoreline change rate BN, developed by Gutierrez et al. (2011), is driven by forces that include relative SLR rate (m/yr), wave height (m), and tide range (m) and constrained by boundary conditions including geomorphology and coastal slope (%) at a coarse 5-km scale. This network was constructed using data sampled and averaged over 5-km segments of coast from Maine to Florida from approximately 1850s-1980s, with exact dates varying by specific locations (Gutierrez et al. 2011).

Geomorphology BN

The geomorphology BN uses information acquired from remote sensing datasets to describe the geomorphology of Assateague Island. This BN was modified from a BN developed by Gutierrez et al. (In review) and calculates the probability of eight geomorphic characteristics (shoreline change rate (m/yr), dune crest height (m), beach width (m), beach height (m), elevation (m), island width (m), presence of anthropogenic modification, and distance to inlet (m), Figure 2, Table 1b). These variables were derived from sample transects spaced 50 m apart that extend across the entire width of the island. For this study, this BN was modified from Gutierrez et al. (In review) to include 4 additional variables that describe

the distance (m) to ocean shoreline (at mean high water line), beach slope (%), habitat type and vegetation type (Figure 2, Table 1b). These additional variables were sampled along the same transects. Variables that were defined locally (elevation, slope, vegetation, and habitat) were calculated at the scale of 5x5-m cells along each transect and associated with the remaining variables that were defined only at the transect-scale. A combination of lidar, aerial photo, and survey data from 1999, 2002, and 2008 were used to train and then implement the BN.

Plover nest selection BN

The plover nest selection BN was constructed using nesting data provided by NPS staff at ASIS from 1999, 2002, and 2008 on the northern 10 km of the island, hereafter 'the North End,' and illustrates the relationship between nest presence and physical variables that are important for nest selection (Table 1c, Figure 2; Gieder et al. 2014). We used the North End to construct the plover nest selection BN because this area has held more than 90% of the total Maryland Piping Plover nesting population since NPS staff at ASIS began monitoring plover nesting populations in 1992 and because detailed data on breeding Piping Plovers and physical habitat variables in this section were the most complete of all other nesting locations on the island.

Each physical variable was derived at either the transect or the 5x5 m resolution and associated with nest locations in 1999, 2002, and 2008, and an equal number of random points generated within plover nesting habitat for each year. The transect-scale variables in the original model (Gieder et al. 2014) included beach width (m), distance (m) to the dune crest and to the dune toe line, distance (m) to the bay and the ocean shoreline (at the mean high water line), distance (m) to the mean low water bay shoreline, distance (m) to moist substrate habitat. The 5-m scale variables included local elevation (m), whether a nest or random point was on or

off an artificial foredune described below, site fidelity, beach slope (%), and vegetation type (Table 1c).

For this study, we modified the BNs presented in Gieder et al. (2014) in order to best support linking the plover BN to the geomorphology BN and to accommodate variation in geomorphology features between the North End and the remainder of Assateague Island. As a starting point, we utilized the simpler version of the plover BN described in Gieder et al. (2014) but added habitat type as an extra variable, because initial analyses of hindcasting without this variable showed poor nest presence and absence predictions across the entire island without these variables. The final model used in this paper included beach width (m), distance to the ocean shoreline (m), elevation (m), habitat and vegetation type, and slope (%; Figure 2) to predict nest presence or absence (see Appendix I for more details).

Linked BN Models

The three independent models make predictions in the form

$$P_{m}(Y_{i}|X) = P_{m}([X_{1,j=1}, X_{1,j=2}, ..., X_{2,j=1}, X_{2,j=2}, \text{etc.}] |Y_{i}) P_{m}(Y_{i}) / P_{m}(X)$$
(eq.1)

where Y_i is a model outcome (e.g., Y = "nest attempt" and $Y_1 =$ 'absent' and $Y_2 =$ 'present'). The result, $P_m(Y_i|X)$, is the posterior probability of this outcome from the mth model (i.e., shoreline change, geomorphology, or plover nest selection). The inputs to this model (which can be actual data or the outputs of the previous model) are denoted by X. The inputs are generally multivariate (e.g., $X_1, X_2, ... X_n$ might correspond to elevation, beach width, etc.) and each input variable is allowed to take on a finite number of states denoted by index j. The left side of equation 1 is Bayes rule and the first term is the likelihood of finding a particular set of inputs given the outcome. The second term is the prior probability of the outcome, and the last term is the probability of finding the particular set of inputs. The algorithm used in Netica factors the terms on the right of equation 1 based on the connections between nodes (e.g, see Charniak 1991 for a simplified description of this calculation). Hence, it is possible to take, e.g., $P_{m-1}(X_{1,j}|W)$ and feed this into the right side of equation 1 anywhere that $P_m(X)$ is required, where W are the inputs to model m-1.

In practice, the shoreline change model was linked to the geomorphology model using the shoreline change rate variable present in both these models. We then used the following matching variables to link the geomorphology model to the plover nest selection models: beach width (m), distance to ocean (at mean high water line, m), elevation (m), slope (%), vegetation type, and habitat type (see Figure 2 and Table 1 a-c).

We changed the bin ranges of certain variables in the geomorphology and plover nest selection BN from ranges presented in Gutierrrez et al. (in review) and Gieder et al. (2014) when we linked these BNs so that inputs and outputs matched (Table 1 a-c). For example, the elevation range (-2.5–29 m) in the geomorphology BN did not match the elevation range in the plover nest selection BN (-0.5–5.8 m) so we changed the elevation range in the plover nest selection BN to (-2.5–29 m) match the range in the geomorphology model. These ranges represent the ranges for all continuous variable data in the BNs, thus they represent ranges for all sample points across the entire island, not just the North End where the Piping Plover model was originally developed. The ranges for the actual data from the North End only from Piping Plover nest sites, and random sites without nests, are included in Table 2 solely for purposes of comparing this known Piping Plover nesting area to other areas where future iterations of these linked models may be applied.

BN hindcasting scenarios

We hindcasted by importing the sampled geomorphic features, obtained from training the geomorphology BN from Assateague Island for a given year and site, into the plover nest selection BN, first for the North End alone and then for the entire island, with 3 focus areas outside of the North End examined for congruence with actual nest presence as described below. We first assessed the plover nest selection BN performance on the North End by computing error rates as in Gieder et al. (2014). Error rates were generated from the actual nest and random point locations previously used to inform the model by quantifying the proportion of nest presence/absence predictions that did not match the actual data. Error rates were further broken down into false positives, false negatives, true positives and true negatives. False positives indicate cases where the plover nest selection BN predicted nest presence when there was no nest presence in the actual data and false negatives indicate cases when the linked models predicted nest absence where there was a nest present in the actual data. True positives and true negatives indicated cases where the linked model's predictions of nest presence and absence matched that of the actual data. We trained the plover nest selection BNs using nesting data from all 3 years (1999, 2002, 2008), then predicted nest probability for each of those years based on input from the observed geomorphology from that year alone, and then compared against actual nests and random points for that year, as per Gieder et al. (2014).

We then hindcasted the probabilities of plover nest presence and absence across the entire Assateague Island, again using inputs from the geomorphology BN, but selected to focus our discussions of prediction accuracy at three areas on Assateague Island outside of the North End in order to test the applicability of the linked BNs in novel areas. We first compared model predictions for each hindcast year to observed nesting site locations in that year for two established nesting sites at CNWR: 1) a narrow strip known as the Overwash and 2) the southern

portion of the island known as the Hook (Figure 1). The Overwash and Hook sites are located on the southern end of Assateague Island. The Overwash is a very narrow (an approximate maximum width of 150 m) strip of land characterized by open beach on the ocean-side, low dunes in the center, and sparsely vegetated moist substrate on the bayside. The Hook is located immediately south of the Overwash and is much wider (an approximate maximum width of 1300 m) compared to the Overwash, with a much larger complex of dunes, wider open beach on the ocean side, and a more varied array of habitats than the Overwash. We then hindcasted at a third mostly-unestablished nesting area that exists in a 19-km portion of ASIS known as the over-sand vehicle (OSV) zone. The OSV-zone is wider and supports a more diverse array of habitats than the North End and plovers only sporadically nested in small numbers (1-5 nests) during the time period of data used to train and hindcast our models. This hindcasting in the OSV-zone allowed us to examine whether the model was correctly predicting potential suitable nesting habitat that was not occupied until some years later.

We presenting the hindcasting results, and the forecasting results described below, by first dividing the island into grids that spanned 1 km of ocean shoreline in length and the width of the island in each of those sections, running south to north along the island. Within each island section, we then calculated the percentage of all points that had a > 0.5 probability of nest presence out of all available points in that section. Although points were sampled every 5 m along transects spaced 50 m apart, the width of the island differed along its length, therefore the number of points within each 1 km section of island differed, thus we look at percentage of each island section suitable for Piping Plover nesting (i.e., p(nest presence) > 0.5). We used the same grid layout for every year that we hindcasted, and color-coded the resulting 53 island sections according to ranges of percentages of points > 0.5 probability of nest presence, from 0-10, 10-20,

20-30, 30-40, 40-50, 50-60, 60-70, 70-80, 80-90, and 90-100% (Figure 3). Thus, if 65% of all points in a 1-km section of island had a p(nest presence) > 0.5, then it was color-coded as the 60-70% category. We used this same procedure to map other variables in the BNs to explore what variables were driving observed nest presence patterns. We used this process to assess the linked BN's predictive capability across the entire island for 1999, 2002, and 2008 and the same process for presenting the forecasting results described below.

Forecasting scenarios: North End

On the North End, we linked the shoreline change, geomorphology, and plover nest selection BNs to develop predictions of nest probabilities for potential future SLR rates and management strategies. We initiated the linkage by predicting shoreline change rate in the shoreline change model under relative SLR rates of 3.0 mm/year, which approximates the average relative SLR for the entire U.S. East Coast, including both barrier island and non-barrier islands, over the past 32–151 years, and 4.1 mm/year, which simulates a higher-than-present coast-wide SLR rate (Zervas 2009, National Oceanic and Atmospheric Administration 2014). While we know that some barrier island areas have higher rates than non-barrier islands (e.g. Duck, NC is 4.6 mm/yr in recent estimates), we use this coast-wide published rate of 3.0 mm/year and one that is approximately 33% higher for this study and will work in future efforts to incorporate higher rates of SLR as described in the discussion of this paper (E.R. Thieler, personal communication). We then input this shoreline change rate into the geomorphology model and then passed the resulting output of the geomorphology model into the plover nest selection model.

We also simulated two possible beach nourishment strategies within the geomorphology model, namely biannual near-shore sand deposition of 60,000 m³ per event (hereafter 'SD') and

the construction of a heavily-notched foredune (i.e., 30% of dune maintained open to allow overwash processes; hereafter 'FD'), based on past, but not necessarily planned future, management activities on Assateague Island and elsewhere along the U.S. Atlantic and Gulf Coasts. Active management in the form of near-shore sand deposition and foredune construction has occurred on the North End in the past (see Schupp et al. 2013) as this section of the island is experiencing high erosion rates as a result of interrupted alongshore sediment transport caused by a permanent jetty constructed to maintain the Ocean City Inlet to the north (-4.3 m/yr after inlet stabilization versus -2.2 m/yr prior, Dean and Perlin 1977, Rosati and Ebersole 1996, Schupp et al. 2007). Following a series of major storm events in January and February 1998, the U.S. Army Corps of Engineers implemented a comprehensive restoration plan to compensate for the erosion caused by the sediment interruption, and constructed an un-notched foredune in 1998 at a height of 2.05 m over the 2.4 km section of the North End that was most vulnerable to overwash (Schupp et al. 2013, Gieder et al. 2014). This restoration plan addressed the sediment starvation in two phases in addition to the un-notched foredune. First, a one-time on-shore sand deposition was completed in 2002 that widened 10.5 km of beach by 30 m to replace approximately 15% (1.4 million m³) of the sand that had been trapped by the inlet since the Hurricane of 1933 opened the inlet. Then, in 2004, a biannual near-shore sand deposition was started as a long-term solution to the sediment interruption; this biannual near-shore sand deposition places 60,000 m³ of sand in the surf zone adjacent to the North End twice yearly since 2004.

We simulated two beach nourishment strategies based on these previous activities: 1) biannual near-shore sand deposition (60,000 m³ twice yearly) along the entire length of the North End (SD) and 2) increased the 2.4 km long foredune height to 4 m with 14, 20 m wide notches

cut into the dune to a height of 2.5 m (FD) with notched areas comprising approximately 30% of the total foredune length. These simulated notches were derived from GIS files of the actual notches that were cut to ground level after the nesting seasons in 2008–2009, thus the simulated notches were in the exact locations as those actually placed on the island in 2008 and 2009 (after the hindcast period of this study), but varied only in height and depth of the actual notch, and assumed that the notches were self-maintaining thus did not change in area or shape over time as occurred in the past when the notches filled in with sand (see Schupp et al. 2013). It is important to emphasize that ASIS cut the notches into the constructed foredune first in November 2008, after the 2008 nesting season, thus habitat changes observed and hindcasted in this study between 1999 and 2008 occurred in the context of an un-notched constructed foredune.

We compared the forecasted predictions of Piping Plover nest presence/absence for all combinations of the two SLR rates and two beach nourishment strategies across the North End using the maps by island section as described above. We calculated the total number of island sections on the North End within each percentage range projected using each of the six scenarios (2 SLR rates x 3 beach nourishment strategies (no management, SD, FD). We compared these areas to those predicted for 2008, 2002, and 1999.

Results

We simulated 6 linked hindcast scenarios (3 years, 2 regions) and 6 forecast scenarios (biannual near-shore sand deposition, heavily-notched foredune construction, or no management using two sea-level rise scenarios) using 1,000,000 observations over the 3 sample periods of 1999, 2002, and 2008. The BN nets themselves spanned 18 770, 5 508 055, and 1 506 948 possible unique conditions for the shoreline change, geomorphology, and plover nest selection BNs (respectively), as defined by the total number of conditional probabilities in each BN.

Hindcasting: Entire island, including North End, OSV, Overwash and Hook nesting areas

Total error rates for the piping plover model on the North End varied from 14.3% when predicting nest presence/absence in 2008 to 21.4% for predicting 2002 nests (Table 3). In all cases, false positives (i.e., predicted nest presence when a nest was not present) dominated the total error (Table 3). The model captured the North End's declining suitability of habitat that occurred between 1999, 2002 and 2008 due to the construction of an un-notched artificial foredune in 1998 and associated vegetation encroachment; in 1999, 2 of 10 island sections had >60% of available points as suitable habitat (i.e., p (nest presence) > 0.5), whereas by 2008, no island sections on the North End had > 40% of available points as suitable habitat. Thus, between 1999 and 2008 on the North End, the model showed that fewer points within each 1-km section of the North End were predicted to be suitable for plover nesting (Figure 4, Table 4; see Gieder et al. 2014).

We found that across the entirety of the island that nests fell in those sections of the island predicted to have the highest proportion of suitable nesting points (Table 4, Figure 5a-c, Appendix II). For example, across the island, nests were predominantly located only on the ASIS North End, ASIS OSV, CNWR Overwash, and CNWR Hook; island sections in each of these nesting regions were predicted to have more points suitable for nesting as compared to the remainder of Assateague Island (Figure 5 a-c). Island sections where < 10% of available nest points were predicted to be suitable rarely held nests. In 2008, 7 piping plover nests were established in an area known as Wild Beach and a nearby artificial nesting area, both on CNWR, even though this zone was predicted to have < 10% of available points suitable for nesting (Table 4). In contrast, an area predicted to have > 10% of points available for nesting in the ASIS-OSV

zone in 2008 held no nests that year, but Piping Plovers did colonize this area in 2012 and 2013 (Figure 6).

Forecasting: linked shoreline change, geomorphology and plover models

We found that, under the SLR rates of 3 mm/year and 4.1 mm/year, all 1-km sections of the North End increased in suitability for Piping Plover nesting as compared to 1999, 2002, and 2008 conditions. We found that 7 of 10 island sections on the North End had > 50% of available points suitable (p(nest presence)> 0.5) for nesting in future scenarios whereas only 3 of 10 sections in 1999, 1 of 10 sections in 2002, and 0 of 10 sections in 2008 had > 50% of total points suitable for nesting. There were no noticeable differences in the future proportion of available suitable habitat between scenarios of 3 mm/year of SLR, 4.1 mm/year of SLR, and both 3 and 4.1 mm/year of SLR with a heavily-notched foredune (FD) (Table 5); in all cases, more points within each section were predicted to be suitable for piping plovers as compared to nesting conditions in 1999, 2002 and 2008 (see Figure 7 versus Figure 4 and Table 5).

While all 6 future scenarios resulted in a substantial increase in areas predicted to be favorable for Piping Plover nest presence as compared to baseline conditions in 1999, 2002 and 2008, we did find one slight difference under a management scenario of 3 mm/yr SLR with frequent near-shore sand deposition (SD); under this scenario there were no island sections that had 70-80% of available points suitable for nesting (Table 5, Figure 7). We found that those island sections that changed between 3 mm/SLR alone and 3/mm SLR with SD differed due to markedly higher proportions of herbaceous and forest/shrub vegetation under the SD scenario as compared to SLR alone (Table 6; Island Sections 43, 44, and 52 had higher proportions of points in herbaceous and woody vegetation under a scenario of SD as compared to SLR alone, corresponding to a decrease in available points for nesting in those island sections). However,
this difference related to frequent near-shore sand deposition was not observed under the scenario of 4.1 mm SLR/yr with frequent sand deposition and the vegetation categories under that scenario were similar to SLR with no management.

Discussion

We developed and tested linked BNs of barrier island shoreline change, geomorphology and Piping Plover nest presence/absence on Assateague Island; this is the first time that the dynamic processes of shoreline change and geomorphological evolution have been linked together and to a model predicting habitat suitability of a threatened wildlife species. We found that the plover nest selection BN successfully predicted nest presence/absence for a majority of nest locations in hindcast scenarios across Assateague Island and predicted the observed decline in habitat suitability for Piping Plover nesting on the North End from 1999 to 2008 in response to geomorphological change related to a suite of beach nourishment strategies implemented over that timeframe, including a one-time on-shore sand placement, biannual near-shore sand deposition, and the construction of an un-notched artificial foredune. We also forecasted for the first time the effects that combinations of 2 SLR rates and 2 beach nourishment strategies would have on future shoreline change, geomorphology and ultimately Piping Plover nest presence/absence and found that under modest SLR rates, suitable nesting habitat is predicted to increase from baseline conditions observed in 1999-2008.

Hindcasting model performance and broad applicability

Our plover nest selection BN accurately predicted the observed shift in nesting habitat quality from 1999 to 2008 on the North End of Assateague Island, where 1999 had the highest proportion of suitable nesting habitat (p[nest presence] > 0.5) and 2008 had the lowest proportion of suitable nesting habitat. As we expanded our hindcasting outside of the area from which the

Piping Plover nest site selection model was developed, we found that the model correctly predicted higher proportions of suitable nesting habitat in sections of established plover nest sites and also in more recent nesting areas that became occupied with nests as the local plover population shifted with habitat changes on the North End (Gieder et al. 2014). The mechanism behind the expansion of plovers into areas predicted to be suitable in the 2008 hindcasting, although no nests were in the area in that year, was likely higher productivity (fledglings/pair) from 2009–2011 on both ASIS and CNWR. Productivity increased from 0.4 to 1.3 on ASIS from 2008-2011 and 0.59 to 1.73 on CNWR from 2008–2010 (K. Holcomb, CNWR, unpublished data and J. Kumer and T. Pearl, ASIS, unpublished data), and thus the fledged chicks were likely to have returned in subsequent years and expanded into the previously unused, but suitable, habitat in the ASIS OSV zone.

While the linked models predicted plover nest presence and absence well on Assateague Island, we may consider further refinements to the shoreline change, geomorphology and plover nest selection models as we expand outside of Assateague Island in hindcasting and forecasting efforts. The plover nest selection model was developed using data from the North End only; this section of Assateague Island is narrower and lower in elevation than the rest of the island (Schupp et al. 2013, Gieder et al. 2014) and many other locations on the U.S. Atlantic Coast. Our hindcasting predictions, and forecasting of areas outside of the North End, could be further improved by training the plover nest selection model with data from other islands with a wider range of geomorphological conditions that affect nest presence or absence, as well as present and future data from Assateague Island itself.

Specific future modifications to the plover BN may include the following. First, we may incorporate the concept of a typical minimum territory size for a nesting Piping Plover as we

know that these birds require some sort of minimum patch size for establishing a nest and will not place nests on a small open patch of sand surrounded by dense vegetation (see Cohen et al. 2009 for information on nesting density and spacing on Long Island, NY as an example); this incorporation of a minimum patch size may help us make more accurate predictions of nest presence at a scale smaller than the 1-km level predictions shown in this study. Second, we plan to attempt to incorporate a variable that would capture time lags in how plovers respond to shifting habitat suitability. For example, Piping Plovers exhibit high site fidelity and thus may not immediately leave an area even if nesting habitat suitability declines, as was observed between 1999 and 2008 on the North End. The inverse is true as well; while habitat suitability in the OSV zone at Assateague Island National Seashore increased between 1999 and 2008, this suitable habitat was not colonized by nesting Piping Plovers until several years later in 2012 and 2013. We may also include a new variable that attempts to describe accessibility of backshore foraging habitats known to be important for fledging success of Piping Plover chicks (Loegering and Fraser 1995). True path distances to backshore foraging areas that incorporate movement barriers (e.g. dense vegetation) to Piping Plovers and their chicks may provide additional detailed information to further improve model predictions.

Predicted responses to SLR and comparison to other studies

Our forecasting results for the North End indicate that under SLR rates of 3–4.1 mm/year, the overall proportion of suitable Piping Plover nesting habitat will increase in 50-100 years (i.e., 2049-2108), compared to the nesting suitability hindcasted in 1999, 2002, and 2008. Our findings are unique in that they are the first demonstration of the ability to link relative SLR and its effects on shoreline change at a local level (i.e., 5-km scale) to dynamic geomorphological changes, influenced both by shoreline change and beach nourishment actions, and derived from

data at a very local level (i.e., 5-by-5m scale) to predictions of wildlife habitat selection at a level relevant to wildlife management decision-making (i.e. 1-km island section scale).

Previous modeling studies on Long Island, New York have similarly found that if human development or modification does not hinder barrier island landscape evolution, Piping Plover nesting habitat may actually increase under SLR ranging from 0.38–1.5 m by 2100 (Seavey et al. 2011); our study only addressed the lower end of this range at this time. Seavey et al. (2011), in particular, did not include geomorphic evolution, such as shoreline change or other impacts of SLR and storms, but rather considered a habitat evolution that was either drowned or could shift upwards on fixed substrate. Our study adds the dynamic response of the substrate via shoreline change, and dynamic geomorphological responses, and local nest site selection. The habitat response is intrinsically modeled as well. For example, we illustrate that the mechanism underlying our predicted increase in Piping Plover suitable habitat is related to changes in vegetation with modest SLR rates compared to those SLR rates and biannual, near-shore sand deposition. The rates of SLR we modeled result in the desired combination of sparse vegetation and accessibility to back barrier moist substrate habitats shown to be important to Piping Plovers along the U.S. Atlantic Coast, thus explaining the increase in the proportion of suitable nesting points within each 1-km section of the North End (Patterson et al. 1991, Loegering and Fraser 1995, Cohen et al. 2009).

Interpretation of future prediction of nest presence

Whereas we predict increases in overall nest site suitability on the North End under these SLR rates, nest site suitability does not necessarily mean sites will be immediately colonized as evident in our 2008 predictions of high suitability for nests in the ASIS-OSV zone, which were not actually used by Piping Plovers until 2012. As a federally-listed species, there may be fewer

Piping Plovers present in an area than habitat available for nesting (U.S. Fish and Wildlife Service 2009). Available habitat may also not be used initially due to high site fidelity in this species that may create a lag time between when a habitat becomes suitable and when plovers use that habitat (Friedrich et al. 2014; Gieder et al. 2014).

We found that, under all scenarios, the proportions of suitable nesting habitat on the North End will increase 50-100 years from the baseline conditions we hindcasted (1999, 2002, 2008). What this increase means for the Piping Plover populations is unclear, however, because more suitable nesting habitat in 50-100 years does not necessarily translate into a productive population of Piping Plovers in the interim or in the future (Rodenhouse 2000). For example, our hindcasting efforts did show that habitat suitability for Piping Plovers declined dramatically between 1999 and 2008; during that time period, a one-time on-shore sand placement, biannual near-shore sand placement, and an un-notched artificial foredune were constructed. We modeled a heavily-notched (i.e., 30% open) foredune as one of our future scenarios given that the past experiences with sand deposition and an un-notched berm led to a rapid (1999 to 2008) decline in habitat suitability for nesting Piping Plovers; the observed decline led ASIS to cut notches into the unnotched dune in 2008 and 2009 in order to improve habitat quality and plover productivity (see Schupp et al. 2013). Our forecasted predictions showed higher suitability of the North End under all SLR and management scenarios as compared to 1999, 2002, and 2008, due to the cumulative effects of 3 - 4.1 mm/yr SLR across that time period. We cannot know under our current modeling framework whether the biannual near-shore sand deposition or heavily-notched foredune (i.e., 30% of foredune open to allow overwash) construction will initially result in declining habitat quality, as observed from 1999 to 2008, but only how those management scenarios along with 3 - 4.1 mm/yr SLR over 50-100 years is predicted to shape habitat in the

future (2049-2108). Our modeling framework is based on historical rates of SLR, averaged over 5-km sections of coast from data averaged between the 1850s -1980s, thus we cannot make short-term, interim predictions of how the piping plover habitat suitability will change. Future work should focus on verifying whether the long-term predictions made here show in shorter-term trend analyses. Future work may also work to compare how short-term shoreline changes, under different beach nourishment scenarios, compare to long-term observed and predicted shoreline changes.

Choice of SLR rates

Our forecast predictions used a 3–4.1 mm/year SLR rate, equivalent to 0.3–0.4 m SLR by 2049-2108, the timeline we modeled in this study. Recent projections estimate that by 2100 global sea-level will range from 0.43–0.73 m higher than present (Intergovernmental Panel on Climate Change 2013). The values used in our forecast are lower than recent forecasted rates (NCA 2012, Horton et al. 2013, Jevrejeva et al. 2014). Because the BNs are based on field data, we are unable to make reliable predictions about the effects of higher SLR rates on shoreline change, geomorphic response, or Piping Plover nest selection on U.S. Atlantic Coast. Updated shoreline change and geomorphological models containing data from regions experiencing higher rates of SLR, such as from the Gulf Coast of the U.S., will improve predictions about Piping Plover nest presence/absence on the U.S. Atlantic Coast under higher SLR rates.

Implications for habitat and species management

Our findings related to SLR rates and beach nourishment strategies have relevant implications for policy-makers today and in the future. We found that a beach nourishment strategy in the form of biannual near-shore sand deposition along the entire North End of ASIS resulted in vegetation encroachment and reduced the proportion of suitable nesting habitat for Piping Plovers under the lower 3 mm SLR rate as compared to the SLR rates without management and the 4.1 mm SLR with management. While there is no such identical management strategy currently proposed for the North End of ASIS, ASIS does artificially receive sand from semi-annual near-shore sand deposition designed to replenish the interruption of sand due to the Ocean City inlet located north of the North End (Schupp et al. 2013, Gieder et al. 2014. Laczo et al. 2014, U.S. Army Corps of Engineers 2014).

Our hindcasted and forecasted modeling results relating near-shore sand deposition to decreased nesting habitat availability for Piping Plovers are consistent with field studies which demonstrated that beach nourishment, usually in concert with other human modifications such as un-notched berm or jetty construction, precedes a decrease in nesting habitat (Cohen et al. 2009; Schupp et al. 2013). Our findings of a decrease in the proportion of nesting habitat on the North End from 1999 to 2008 after the construction of an un-notched artificial foredune and biannual nearshore sand placement further allude to potential negative effects of some beach management strategies.

We caution that our forecasts showing an increase in the proportion of future suitable nesting habitat under modest sea-level rise rates and beach nourishment should be interpreted in the context of known, past negative impacts of beach nourishment on piping plover habitat suitability. Negative effects on nesting habitat suitability in the short term could affect the ability of future piping plover populations to respond to increased habitat suitability due to SLR in the long-term. Thus, an increase in future long-term habitat suitability may not yield benefits on a population-level if short-term effects of beach management have negative population consequences.

Our findings provide an important starting point for further developing and testing of this tool that can be used to predict how Piping Plover nest habitat will change with proposed efforts to use beach nourishment as part of a suite of human modifications planned in response to threats of SLR or tropical storm events (see U.S. Fish and Wildlife Service 2009 for a review of existing or proposed inlet and shoreline stabilization projects). While we did model the future effects of SLR in combination with biannual near-shore sand placement and a heavily notched foredune, we must also model the effects of on-shore sand placement and un-notched foredune, and caution that our current results cannot be used to make inferences about those or other potential beach management activities until predictions are further verified with both short-term and longterm data from specific scenarios and island sites. Further analyses of the geomorphology output under varying scenarios of sand placement, foredune height, and notch creation should be informative to managers considering the use of these strategies for storm protection and would show the implications of proposed approaches for nesting Piping Plovers. It is important to reiterate that while we showed no differences in future conditions with or without a heavilynotched foredune (i.e. 30% of foredune notched and open to overwash), due to the accumulated geomorphological effects of 3-4.1 mm/yr SLR over 50-100 years, we cannot make predictions about shorter-term changes under this current modeling framework. We know from hindcasting, that over a short-time period, sand deposition and an un-notched foredune led to declining habitat suitability, thus without the cumulative effects of 50-100 years of SLR, we should assume the same short-term decline in habitat suitability would be observed.

Our demonstration of an ability to make fine- to coarse-scale, site-specific future predictions of island geomorphology and Piping Plover habitat using relative SLR will be useful

to managers coast-wide, and these linked models are currently being tested and expanded to other Piping Plover nesting locations, including sites from Massachusetts to North Carolina.

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Zhang K, Leatherman S (2011) Barrier Island Population along the US Atlantic and Gulf Coasts. J Coast Res 27:356–363. Table 1a: Variables and bin categories for the shoreline change Bayesian Network included in our linked model used to predict the effect of changing geomorphological variables on barrier islands on Piping Plover (*Charadrius melodus*) nest presence/absence.

Variable		Bir	n Categories		
v allable	1	2	3	4	5
Relative sea- level rise rate (mm/yr)	0-1.8	1.8-2.5	2.5-2.95	2.95-3.16	3.16-4.1
Coastal slope (%)	0-0.025	0.025-0.04	0.04-0.07	0.07-0.2	0.2- 0.411
Tidal range (m)	0-1	1-2	2-4	4-6	6-10
Mean wave height (m)	0-0.55	0.55-0.85	0.85-1.05	1.05-1.25	1.25-1.6
Geomorphology ^a	Geo 1	Geo 2	Geo 3	Geo 4	Geo 5
Shoreline change rate (m/yr)	-25-(-2)	-2-(-1)	-1-1	1-2	2-30

^a Geomorphology variable categories include Geo 1, very low risk, rocky, cliffed coasts, fjords; Geo 2, low-risk, medium cliffs, indented coasts; Geo 3, moderate risk, low cliffs, glacial drift, alluvial plains; Geo 4, high-risk, cobble beaches, estuarine and lagoonal coasts; Geo 5, very high risk, barrier beaches, sand beaches, salt marsh, mud flats, deltas, mangroves, coral reefs. See Gutierrez et al. (2011) for further details.

Table 1b: Variables and bin categories for the geomorphology Bayesian Network included in our linked model used to predict the effect of changing geomorphological variables on barrier islands on Piping Plover (*Charadrius melodus*) nest presence/absence. We parameterized the network using a three-year dataset from 1999, 2002, and 2008 on Assateague Island National Seashore, MD. See Gutierrez et al. In Review for more details on variables.

			Bin	Categories			
Variable	1	2	3	4	5	6	7
Shoreline change rate (m/yr)	-10-(-2)	-2-(-1)	-1-1	1-2	2-30	n/a	n/a
Island width (m)	0-500	500-1000	1000-1500	1500- 2000	2000- 4500	n/a	n/a
Beach height (m)	0-1	1-1.25	1.25-1.5	1.5-2	2-3	n/a	n/a
Distance to inlet (m)	0-11500	11500- 17000	17000- 21500	21500- 26500	26500- 32070	n/a	n/a
Dune crest height (m)	0-2.4	2.4-3.3	3.3-4.3	4.3-5.1	5.1-7.5	n/a	n/a
Anthropogenic modification	None	Construction	Occasional	ConstpON	Frequent	FreqpConst	n/a
Elevation (m)	-2.5-(- 0.5)	-0.5-0.5	0.5-1.5	1.5-2.5	2.5-3.5	3.5-29	n/a
Beach width (m)	0-50	50-100	100-150	150-200	200-600	n/a	n/a
Mean beach slope (%)	0-2.5	2.5-5	5-7.5	7.5-20	20-90	n/a	n/a
Distance to mean high water ocean (m)	0-100	100-200	200-300	300-400	400-500	500-1000	1000- 4400

Table 1c. Variables and bin categories for the Piping Plover Bayesian Network included in our complete linked model used to predict the effect of changing geomorphological variables on barrier islands on Piping Plover (*Charadrius melodus*) nest presence/absence. The simple model used in this study use these same variables and ranges, but excludes site fidelity, distance to bay (at mean high water line), and distance to the dune crest. We parameterized the network using a three-year dataset containing observed nest locations and random points that did not contain nests on Assateague Island National Seashore, MD.

Variable ^a	Numb V	er of Ob Values ^b (1	served n)	Bin Categories ^c						
	1999	2002	2008	1	2	3	4	5	6	7
Beach width (m)	119	117	140	0–50	50-100	100–150	150-200	200–600	n/a	n/a
Distance to dune crest (m)	144	122	140	-100–0	0–100	100–200	200–400	400–600	600–1000	n/a
Distance to bay at MHW (m)	144	122	140	0–100	100–200	200-300	300-400	400-1000	n/a	n/a
Distance to ocean at MHW (m)	144	122	140	0–100	100–200	200–300	300-400	400–500	500-1000	1000-4400
Elevation (m)	144	122	140	-2.5-0.5	-0.5-0.5	0.5–1.5	1.5-2.5	2.5-3.5	3.5–29	n/a
Nest attempt	144	122	140	Absent	Present	n/a	n/a	n/a	n/a	n/a
Site fidelity	144	122	140	None	Potential	n/a	n/a	n/a	n/a	n/a

Slope (%)	144	110	140	0–2.5	2.5-5.0	5-7.5	7.5–20	20–90	n/a	n/a
Habitat type	139	117	139	Wetland	Shrub/Forest	Sandy barrier	Unknown	n/a	n/a	n/a
Vegetation type	144	122	140	Water	Sparse	Herbaceous	Shrub/Forest	Shellbed	n/a	n/a

^a "Beach width (m)" is the horizontal distance between the dune-toe boundary and the mean low water (MLW) line; "Distance to dune crest (m)" is the perpendicular distance from the dune high boundary to a nest or random point without nest; "Distance to bay at MHW (m)" is the perpendicular distance from the mean high water bay boundary to a nest or random point without nest; "Distance to ocean at MHW(m)" is the perpendicular distance from the mean high water ocean boundary to a nest or random point without nest; "Elevation (m)" is the vertical height above sea-level of a nest or random point without nest; "Nest attempt" indicates a nest (present) or random point without nest (absent); "Site fidelity" indicates whether a nest or random point without nest is within 75 m (potential) or not (none) of a nest or random point without nest; "Habitat type" is the general habitat type at the nest or random point without nest; "Vegetation type" is the general type and density of vegetation at a nest or random point without nest.

^b Observed values of '0' indicate variables for which no data were available and thus were not included in the network. Variables that have observed values that were lower than the highest observed value for that year indicate that a certain proportion of data was not available. These variables were still included in the network because Bayesian networks are designed to accommodate missing data. ^c Bin categories are non-overlapping. Table 2. Average and range for the continuous variables (excluding categorical variables of site fidelity, habitat type, vegetation type) extracted from field- and remotely-sensed data on the North End of Assateague Island National Seashore, at Piping Plover nest sites, and sites without nests, that were used to inform the plover nest selection BN.

Variabla ^a		1999		2002		2008
vallable	Average	Range	Average	Range	Average	Range
Beach width (m)	73.21	31.43-179.97	85.85	19.78–193.29	99.02	35.63-189.78
Distance to dune crest (m)	176.92	0.60–544.99	151.33	1.14-527.96	109.80	2.35-445.80
Distance to bay (m)	177.82	2.33-483.53	210.76	1.60-510.86	222.07	0.85-462.66
Distance to ocean (m)	246.68	6.10-614.18	231.63	19.29-608.00	211.27	12.58-622.81
Elevation (m)	1.03	-0.08-3.48	1.16	0.08-3.12	1.27	-0.32-3.33
Slope (%)	4.53	1.00-39.18	2.59	1.08-8.94	3.00	0.92-15.74

^a "Beach width (m)" is the horizontal distance between the dune-toe boundary and the mean low water (MLW) line; "Distance to dune crest (m)" is the perpendicular distance from the dune high boundary to a nest or random point without nest; "Distance to bay (m)" is the perpendicular distance from the mean high water bay boundary to a nest or random point without nest; "Distance to ocean (m)" is the perpendicular distance from the mean high water ocean boundary to a nest or random point without nest; "Elevation (m)" is the vertical height above sea-level of a nest or random point without nest; "Slope (%)" is the average rise over run within a 5 m radius of a nest or random point without nest.

Table 3. Error (%) associated with predictions of Piping Plover (*Charadrius melodus*) nest site presence/absence. Predictions were generated from the linked Bayesian networks containing the geomorphology model and the Piping Plover nest selection model for the North End of Assateague Island National Seashore, MD in 1999, 2002, and 2008.

		Error (%)	b	
Model ^a		False	False	
	lotal	positives	negatives	
Dallyrs_P08	14.3	11.4	2.9	
Dallyrs_P02	21.4	14.8	6.6	
Dallyrs_P99	13.9	12.5	1.4	

^a "D" indicates the year of data used to generate the conditional probabilities for the model, in this case all three years, "P" indicates the year from which model probabilities were derived, 2008 (08), 2002 (02), or 1999 (99).

^b Total error is the percentage of the model predictions that did not match the observed data. False positives indicate the percentage of that total error attributed to the model predicting a nest being present when there was no actual nest observed. False negatives indicate the percentage of the total error attributed to the model predicting a nest absence when there actually was a nest observed. The combined percentages of false negatives and false positives equals 100% total error.

Table 4. Number of Piping Plover nests (*Charadrius melodus*) in 1999, 2002, and 2008 found in different regions of Assateague Island, MD and how those nests were located within 1-km subsections of island that were categorized by the proportion of available suitable nesting sites (p(nest presence) > 0.5) in each 1-km section.

<u>Proportion of available points in a 1-km section of island where p(nest presence) > 0.5°</u>												
			_		_					-		Total
	Island											#
Year ^a	Region ^b	0 - 10	10 - 20	20 - 30	30 - 40	40 - 50	50 - 60	60 - 70	70 - 80	80 - 90	90 - 100	Nests
2008	North End	0	20	16	34	-	-	-	-	-	-	70
	OSV	1	1	-	-	-	-	-	-	-	-	2
	WB/ANA	7	3	0	0	20	-	-	-	-	-	10
	Overwash	0	6	0	0	0	-	-	-	-	-	6
	Hook	0	14	0	0	20	-	-	-	-	-	34
2002	North End	0	0	1	23	19	15	-	-	-	-	58
	OSV	0	3	-	-	-	-	-	-	-	-	3
	Overwash	0	0	5	0	0	0	7	-	-	-	12
	Hook	0	11	5	0	0	0	0	-	-	-	16
1999	North End	4	0	3	5	31	12	17	-	-	-	72
	OSV	2	0	0	-	-	-	-	-	-	-	2
	Overwash	0	0	6	-	-	-	-	-	-	-	6
	Hook	0	0	9	-	-	-	-	-	-	-	9

^a Year of nesting and year of model predictions.

^b Sub-regions of Assateague Island where nesting occurred included ASIS-North End; ASIS-OSV, Over-sand vehicle area; CNWR-WB/ANA, Wild Beach Artificial Nesting Area; CNWR-Overwash; CNWR-Hook. No other nests were located on Assateague Island in any other area during these years.

^c Model predictions of nest site suitability were calculated for each 1-km section of Assateague Island as the proportion of all available points that were suitable (p(nest presence)>0.5) for piping plover nesting. For example, 34 nests on the North End in 2008 fell into 1-km island sections where overall between 30-40% of nest points were predicted to have p(nest presence)>0.5. A (-) means no island sections were predicted to fall in that range of available suitable points.

Table 5. Number of 1-km sections (out of 10 total sections) of the North End of Assateague Island, MD as characterized by the proportion of available suitable nesting sites (p(nest presence) > 0.5) for Piping Plovers (*Charadrius melodus*) in each 1-km section for past conditions in 2008, 2002, and 1999 and 6 future scenarios, including sea-level rise of 3 and 4.1 mm/yr, and management options of frequent, biannual, near-shore sand deposition (SD) and heavily-notched foredune (FD) to 50-100 years from the baseline (2049-2108). The predicted output is based on linking shoreline change, geomorphology, and piping plover nest selection models.

Vear or Scenario		Propo	rtion of av	ailable po	ints in a 1-	km sectio	n of island	where p(nest presei	$nce) > 0.5^{b}$	
Predicted ^a											# Island
Traitied	0 - 10	10 - 20	20 - 30	30 - 40	40 - 50	50 - 60	60 - 70	70 - 80	80 - 90	90 - 100	Sections
2008	-	5	3	2	-	-	-	-	-	-	10
2002	1	1	1	4	2	1	-	-	-	-	10
1999	2	-	2	1	2	2	1	-	-	-	10
Future 3 mm SLR	-	-	-	-	3	3	2	2	-	-	10
Future 4.1 mm SLR	-	-	-	-	3	3	2	2	-	-	10
Future 3 mm SLR											
with SD	-	-	-	-	3	3	4	-	-	-	10
Future 3 mm SLR											
with FD	-	-	-	-	3	3	2	2	-	-	10
Future 4.1 mm SLR											
with SD	-	-	-	-	3	3	2	2	-	-	10
Future 4.1 mm SLR											
with FD	-	-	-	-	3	3	2	2	-	-	10

^a Year or scenario of model predictions.

^b Model predictions of nest site suitability were calculated for each 1-km section of Assateague Island as the proportion of all

available points that were suitable (p(nest presence)>0.5) for piping plover nesting. For example, 2 of 10 1-km island sections on the

North End in 2008 fell into the categorization that overall between 30-40% of nest points were predicted to have p(nest presence)>0.5. A (-) means no island sections were predicted to fall in that range of available suitable points.

Table 6. Proportion of points by 1-km sections of the North End of Assateague Island National Seashore, MD (from the southernmost section # 43 to the northernmost section # 52) that were categorized as sparse, herbaceous, or woody vegetation under a future scenario of 3 mm/yr SLR and 3 mm/yr SLR with biannual near-shore sand deposition (SD). The predicted output is based on linking a shoreline change, geomorphology, and piping plover nest selection models.

	Spa	arse ^a	He	rbaceous	Woody		
Island		3mm/yr		3mm/yr with		3mm/yr	
Section	3mm/yr	with SD	3mm/yr	SD	3mm/yr	with SD	
43	72	52	2	15	7	12	
44	96	54	1	21	3	24	
45	52	45	0	5	0	2	
46	67	64	13	14	4	5	
47	62	65	27	23	4	4	
48	77	76	12	12	7	8	
49	77	71	9	15	8	7	
50	58	55	19	23	11	11	
51	46	41	15	21	12	10	
52	100	76	0	24	0	0	

^aThe vegetation area categories include sparse vegetation defined as <20% continuous ground cover within a minimum area of 25 m²,

herbaceous vegetation defined as >20% continuous ground cover within a minimum area of 25 m², woody vegetation generally

defined as pockets of shrubs or trees that are visibly discernable from a distance



Fig. 1. We generated Piping Plover (*Charadrius melodus*) nesting probabilities using three linked models that considered shoreline change due to sea level rise (SLR) and storms, barrier island geomorphological variables and plover nest presence/absence. Initial models were developed with data from (A) the northern 10 km of Assateague Island National Seashore, MD. Nesting probabilities were then generated across the entire island and compared especially to other nesting locations on the island, including (B) the over-sand vehicle zone of Assateague Island National Seashore and areas known as the (C) Overwash and (D) Hook at Chincoteague National Wildlife Refuge, VA.



Figure 2. Schematic representation of three independent Bayesian Networks (BNs) constructed using Netica software (Norsys, 1992-2010) for 1) the shoreline change model (blue oval), 2) the geomorphology model (nude oval), and 3) the Piping Plover (*Charadrius melodus*) nest selection model (green oval). Shoreline change rate, an output of the shoreline change model, was used as an input of the geomorphology model (denoted by overlapping blue area). The geomorphology model and the Piping Plover nest selection model were linked through several shared variables (denoted by overlapping green area). The final outcome of nest presence or absence probability from this linked network is denoted by the nest attempt variable outlined in yellow.



Figure 3. An example of the color-coded map developed to show the percent of total points with p > 0.5 predicted Piping Plover (*Charadrius melodus*) nest presence probability within 1 km island sections of Assateague Island, MD and VA. The lines of dots illustrate points sampled every 5 m along transects spaced 50 m apart, with black dots representing all points with a > 0.5 nest presence probability and white dots representing all points with $a \le 0.5$ nest presence

probability. This light blue, green, and red color of the grids in this image illustrate that 10-20, 20-30, and 50-60 % of the total points within each respective grid had p > 0.5 nest presence probability.



Figure 4. Percent of total points per 1 km island section with p > 0.5 predicted Piping Plover (*Charadrius melodus*) nest presence probability for 1999 (1), 2002 (2), and 2008 (3) on the northern 10 km of Assateague Island, MD. Percent ranges for each grid are displayed in color and actual nest locations for each respective year are depicted by the black and white circles.






Figure 5. Percent of total points per 1 km island section with p > 0.5 predicted Piping Plover (*Charadrius melodus*) nest presence probability for 1999 (1), 2002 (2), and 2008 (3) on Assateague Island, MD and VA. Percent ranges for each grid are displayed in color and actual nesting areas are outlined by black boxes. These areas include (A) the northern 10 km of Assateague Island National Seashore, MD, (B) a portion of the over-sand vehicle zone of Assateague Island National Seashore and areas known as the (C) Overwash and (D) Hook at Chincoteague National Wildlife Refuge, VA.



Figure 6. Percent of total points per 1 km section of island with p > 0.5 predicted Piping Plover (*Charadrius melodus*) nest presence probability for 2008 in the over-sand vehicle (OSV) section of Assateague Island National Seashore, MD, versus actual nest locations in 2012 (squares) and 2013 (circles). No nests were present in this area in 2008 despite higher percent values than the surrounding area; however, a majority of OSV piping plover nests were established in this area in 2012 and 2013, respectively.



Figure 7. Percent of total points per 1 km length grid with > 0.5 predicted Piping Plover (*Charadrius melodus*) nest presence probability approximately 50-100 years in the future on the northern 10 km of Assateague Island, MD, under 1) 3 mm/year sea-level rise and 2) 3 mm/yr sea-level rise and a management strategy of biannual sand deposition (SD) along the entire North End. Areas circled in blue indicate the island sections (from section 43 in the South to 53 in the North) that changed from 3 mm/year sea-level rise to the same sea-level rise with frequent sand deposition. Plates 3 and 4 show corresponding percent (%) of total points within each grid that had herbaceous vegetation type (i.e. vegetation density >20% within minimum 25 m²) under 3) 3 mm/yr sea-level rise and a management strategy of frequent sand deposition along the entire North End.

Appendix I

Objective: To compare predicted Piping Plover (*Charadrius melodus*) nest presence probability for a complete and simple version of a piping plover nest selection model for 2008 on Assateague Island, MD and VA in order to decide the best version of the Piping Plover model to use in forecasting.

Methods

For this study, we modified the BNs presented in Gieder et al. (2014) in order to support linking the plover BN to the geomorphology BN and to accommodate variation in geomorphology features between the northern 10 km of Assateague Island (North End) and the remainder of the island. As a starting point, we utilized both the complete and a simpler version of the plover BN described in Gieder et al. (2014) to evaluate the linked BNs. The complete model included the variables in Gieder et al. (2014) except for distance (m) to the dune toe, distance (m) to the mean low water bay shoreline, distance (m) to moist substrate habitat, and whether a nest or random point was on or off an artificial foredune located on the North End (Figure 1). We excluded the first three variables because data was not consistently available for sample points across the entire island and we excluded the last variable (the artificial foredune) because this feature only occurred on the North End and thus data for this variable did not pertain to sample points at other locations on the island. In this paper, we also tested a simple model that included the variables shown in Figure 2, but excluded site fidelity, distance to bay (at mean high water line), and distance to the dune crest as these variables require lidar data or data on nest locations from the preceding year, which are not always available to constrain the model. We compared the complete and simple versions of the plover nest selection models by

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developing hindcasting predictions of nest presence suitability using both the complete and simple version of a piping plover nest selection model for 2008 and comparing these results by dividing the island into grids that spanned 1 km of ocean shoreline, running north to south and calculating the percentage of points within each grid that had a > 0.5 probability of nest presence. Although points were sampled consistently every 5 m along transects spaced 50 m apart, the width of the island differed along its length, therefore the number of points within each 1 km length grid differed. We used the same grid layout across the entire island for both versions of the model, and color-coded the resulting 53 grid sections according to ranges of percentages from 0-10, 10-20, 20-30, 30-40, 40-50, 50-60, 60-70, 70-80, 80-90, and 90-100 percent. Thus, if 65% of all points in a 1-km section of island had a p(nest presence) > 0.5, then it was colorcoded as the 60-70% category. We compared these results across the entire island and also focused on nesting areas, including the northern 10 km (North End) of Assateague Island National Seashore, MD, a portion of the over-sand vehicle (OSV) zone of Assateague Island National Seashore (ASIS), MD and areas known as the Overwash and Hook at Chincoteague National Wildlife Refuge (CNWR), VA.

Results

The complete version of the nest selection model had a much lower overall percent of total points per 1 km island section with > 0.5 predicted Piping Plover (*Charadrius melodus*) nest presence probability compared to the simple model version (Figure 1). With the complete version, most (49 of 53) of the island sections had 0-10% of points within each grid with a > 0.5 probability of nest presence. The remaining 4 island sections had 10-20% of points within each island section with a > 0.5 probability of nest presence. Comparatively, the simple model had only 17 of the 53 island sections with 0-10% of points within each section that had a > 0.5

probability of nest presence (Table 1). Percentages of points within each island section with a > 0.5 probability of nest presence ranged up to 30-40% with the simple model. A majority of this increase in proportion of suitable nesting points occurred in the nesting areas we focused on in this study (Figure 2). On the North End at ASIS, the simple model predictions showed 2 island sections with 30-40%, 3 island sections with 20-30%, and the remaining 5 island sections with 10-20% of points within each section with a > 0.5 probability of nest presence. In the OSV zone at ASIS, the simple model predictions showed a higher number of island sections with 10-20% of points within each section with a > 0.5 probability of nest presence compared to the complete model predictions. On CNWR, the simple model predictions showed the same percentage of points within each island section with a > 0.5 probability of nest presence. Furthermore, the simple model predictions also showed higher percentages of points within each island section with a > 0.5 probability of nest presence in other nesting areas on the island, whereas the complete model predictions did not. These other nesting areas included an area immediately north of the Overwash on CNWR (Public Beach) that is frequently overwashed during severe storm events and another area further north on CNWR (Wild Beach Artificial Nesting Area) that includes an artificially created nesting area and a nesting area that regularly has one to two nests in a breeding season (Figure 2).

Conclusions

Overall, the complete model nest presence predictions underestimated available Piping Plover nesting area because many actual nesting areas did not show any difference in the percentage of points within each island section with a > 0.5 probability of nest presence. The simple model nest presence predictions more accurately reflected the actual used nesting areas across the entire island. Furthermore, a simpler version of the model would be better suited for expanding the

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model applications beyond Assateague Island because lidar data for barrier island locations along the U.S. Atlantic coast is variable and often incomplete. Finally, the most parsimonious model is desired by researchers as well as managers. For these reasons, we used the simple model version in all our analyses of hindcasting and forecasting scenarios.

Table 1. Number of 1-km sections (out of 53 total sections) of Assateague Island, MD as characterized by the proportion of available suitable nesting sites (p(nest presence) > 0.5) for Piping Plovers (*Charadrius melodus*) in each 1-km section for past conditions in 2008 for a complete and simple version of a Piping Plover nest selection model. The predicted output is based on linking a shoreline change, geomorphology, and piping plover nest selection models.

-	Island Region ^b	Proportion of available points in a 1-km section of island where $p(nest presence) > 0.5b$										
Year ^a		0 - 10	20-Oct	20 - 30	30 - 40	40 - 50	50 - 60	60 - 70	70 - 80	80 - 90	90 - 100	Total # Grids
2008 complete model	Entire	49	4	-	-	-	-	-	-	-	-	53
	North End	6	4	-	-	-	-	-	-	-	-	10
	OSV	9	-	-	-	-	-	-	-	-	-	9
	Wild Beach	2	-	-	-	-	-	-	-	-	-	2
	Public Beach	2	-	-	-	-	-	-	-	-	-	2
	Overwash	2	-	-	-	-	-	-	-	-	-	2
	Hook	2	-	-	-	-	-	-	-	-	-	2
2008 simple model	Entire	17	27	4	5	-	-	-	-	-	-	53
	North End	0	5	3	2	-	-	-	-	-	-	10
	OSV	3	6	-	-	-	-	-	-	-	-	9
	Wild Beach	0	0	1	1	-	-	-	-	-	-	2
	Public Beach	0	2	-	-	-	-	-	-	-	-	2
	Overwash	0	1	0	1	-	-	-	-	-	-	2
	Hook	0	1	0	1	-	-	-	-	-	-	2

^a Year and version of model.

^b Model predictions of nest site suitability were calculated for each 1-km section of Assateague Island as the proportion of all available points that were suitable (p(nest presence)>0.5) for piping plover nesting. For example, 2 of 10 1-km island sections on the

North End in the 2008 simple model fell into the categorization that overall between 30-40% of nest points were predicted to have p(nest presence) > 0.5. A (-) means no island sections were predicted to fall in that range of available suitable points.



Figure 1. Schematic representation of three independent Bayesian Networks (BNs) constructed using Netica software (Norsys, 1992-2010) for 1) the shoreline change model (blue oval), 2) the geomorphology model (orange oval), and 3) the complete Piping Plover (*Charadrius melodus*) nest selection model (yellow oval). The simple version of the piping plover nest selection model excluded site fidelity, distance to the mean high water bay line (distance to bay), and distance to the dune crest. Shoreline change rate, an output of the shoreline change model, was used as an input of the geomorphology model (denoted by overlapping blue-orange area). The geomorphology model and the Piping Plover nest selection model were linked through several shared variables (denoted by overlapping orange-yellow area).



Figure 2. Percent of total points per 1 km length grid with > 0.5 predicted Piping Plover (*Charadrius melodus*) nest presence probability for a complete (1) and simple (2) version of a piping plover nest selection model for 2008 on Assateague Island, MD and VA. Percent ranges for each grid are displayed in color and actual nesting areas are outlined by black boxes. These areas include (A) the northern 10 km of Assateague Island National Seashore, MD, (B) a portion of the over-sand vehicle zone of Assateague Island National Seashore and areas known as the (C) Wild Beach Artifical Nesting Area, (D) Public Beach, (E) Overwash and (F) Hook at Chincoteague National Wildlife Refuge, VA.

Appendix II. Number of 1-km sections (out of 53 total sections) of Assateague Island, VA and MD as characterized by the proportion of available suitable nesting sites (p(nest presence) > 0.5) for Piping Plovers (*Charadrius melodus*) in each 1-km section for past conditions in 2008, 2002, and 1999.

	Proportion of available points in a 1-km section of island where $p(nest presence) > 0.5^{b}$										
Year Predicted ^a											# Island
	0 - 10	10 - 20	20 - 30	30 - 40	40 - 50	50 - 60	60 - 70	70 - 80	80 - 90	90 - 100	Sections
2008	17	27	4	4	1	-	-	-	-	-	53
2002	27	15	2	5	2	1	1	-	-	-	53
1999	35	6	6	1	2	2	1	-	-	-	53

^a Year of model predictions.

^b Model predictions of nest site suitability were calculated for each 1-km section of Assateague Island as the proportion of all available points that were suitable (p(nest presence)>0.5) for piping plover nesting. For example, 35 of 53 1-km island sections on the Assateague island as a whole in 1999 fell into the categorization of having 0-10% of points predicted to have p(nest presence)>0.5. A
(-) means no island sections were predicted to fall in that range of available suitable points.

Chapter 4: Conservation and management implications and next steps

Conservation and Management Implications of Completed Work:

We 1) reviewed the literature, 2) met extensively with site managers for Assateague Island National Seashore and Chincoteague National Wildlife Refuge, 3) visited sites on Assateague Island to collect field data on habitat features of piping plover nest points and random points without nests, and 4) compiled historical data (1998-2013) on piping plover nests, habitat maps, aerial photography, and lidar in order to build and parameterize the island geomorphology and piping plover nest site selection models. Whereas data on piping plover nests was available back to 1998, there were only 3 years with robust physical data (e.g. aerial photography, lidar) during the nesting season and thus we built and tested the models using data from 1999, 2002, and 2008. In coordination with USGS, we built and used hindcasting scenarios for these three years to test models of island geomorphology and piping plover nest site selection individually, and linked together. We then used linked models of the effects of sea-level rise on shoreline change, island geomorphology, and piping plover nest site selection to forecast piping plover nest site presence and absence over a time period of 50-100 years from present, using two sea-level rise rates and two options for management actions.

We have published one peer-reviewed paper (see chapter 2) and two others are in preparation/revision (see chapter 3 and chapter 5 for summary of products). In each of those papers, we discuss management implications of our work in the discussion sections in detail. In this section, we highlight our findings related to forecasting resilience of piping plover nest presence in the face of all combinations of two sea-level rise scenarios and 3 management scenarios.

Hindcasting model performance and desired improvements to models for future work

While our linked models predicted plover nest presence and absence well on Assateague Island, we may consider further refinements to the shoreline change, geomorphology and plover nest selection models as we expand outside of Assateague Island in hindcasting and forecasting efforts. The plover nest selection model was developed using data from the North End only; this section of Assateague Island is narrower and lower in elevation than the rest of the island (Schupp et al. 2013, Gieder et al. 2014) and many other locations on the U.S. Atlantic Coast. Our hindcasting predictions, and forecasting of areas outside of the North End, could be further improved by training the plover nest selection model with data from other islands with a wider range of geomorphological conditions that affect nest presence or absence, as well as present and future data from Assateague Island itself.

Specific future modifications to the plover BN may include the following. First, we may incorporate the concept of a typical minimum territory size for a nesting Piping Plover as we know that these birds require some sort of minimum patch size for establishing a nest and will not place nests on a small open patch of sand surrounded by dense vegetation (see Cohen et al. 2009 for information on nesting density and spacing

on Long Island, NY as an example); this incorporation of a minimum patch size may help us make more accurate predictions of nest presence at a scale smaller than the 1-km level predictions shown in this study. Second, we plan to attempt to incorporate a variable that would capture time lags in how plovers respond to shifting habitat suitability. For example, Piping Plovers exhibit high site fidelity and thus may not immediately leave an area even if nesting habitat suitability declines, as was observed between 1999 and 2008 on the North End. The inverse is true as well; while habitat suitability in the OSV zone at Assateague Island National Seashore increased between 1999 and 2008, this suitable habitat was not colonized by nesting Piping Plovers until several years later in 2012 and 2013. We may also include a new variable that attempts to describe accessibility of backshore foraging habitats known to be important for fledging success of Piping Plover chicks (Loegering and Fraser 1995). True path distances to backshore foraging areas that incorporate movement barriers (e.g. dense vegetation) to Piping Plovers and their chicks may provide additional detailed information to further improve model predictions.

Predicted responses to SLR and comparison to other studies

Our forecasting results for the North End indicate that under SLR rates of 3–4.1 mm/year, the overall proportion of suitable Piping Plover nesting habitat will increase in 50-100 years (i.e., 2049-2108), compared to the nesting suitability hindcasted in 1999, 2002, and 2008. Our findings are unique in that they are the first demonstration of the ability to link relative SLR and its effects on shoreline change at a local level (i.e., 5-km scale) to dynamic geomorphological changes, influenced both by shoreline change and beach nourishment actions, and derived from data at a very local level (i.e., 5-by-5m scale) to predictions of wildlife habitat selection at a level relevant to wildlife management decision-making (i.e. 1-km island section scale).

Previous modeling studies on Long Island, New York have similarly found that if human development or modification does not hinder barrier island landscape evolution, Piping Plover nesting habitat may actually increase under SLR ranging from 0.38–1.5 m by 2100 (Seavey et al. 2011); our study only addressed the lower end of this range at this time. Seavey et al. (2011), in particular, did not include geomorphic evolution, such as shoreline change or other impacts of SLR and storms, but rather considered a habitat evolution that was either drowned or could shift upwards on fixed substrate. Our study adds the dynamic response of the substrate via shoreline change, and dynamic geomorphological responses, and local nest site selection. The habitat response is intrinsically modeled as well. For example, we illustrate that the mechanism underlying our predicted increase in Piping Plover suitable habitat is related to changes in vegetation with modest SLR rates compared to those SLR rates and biannual, near-shore sand deposition. The rates of SLR we modeled result in the desired combination of sparse vegetation and accessibility to back barrier moist substrate habitats shown to be important to Piping Plovers along the U.S. Atlantic Coast, thus explaining the increase in the proportion of suitable nesting points within each 1-km section of the North End (Patterson et al. 1991, Loegering and Fraser 1995, Cohen et al. 2009).

Implications for habitat and species management

Our findings related to SLR rates and beach nourishment strategies have relevant implications for policy-makers today and in the future. We found that a beach nourishment strategy in the form of biannual near-shore sand deposition along the entire North End of ASIS resulted in vegetation encroachment and reduced the proportion of suitable nesting habitat for Piping Plovers under the lower 3 mm SLR rate as compared to the SLR rates without management and the 4.1 mm SLR with management. While there is no such identical management strategy currently proposed for the North End of ASIS, ASIS does artificially receive sand from semi-annual near-shore sand deposition designed to replenish the interruption of sand due to the Ocean City inlet located north of the North End (Schupp et al. 2013, Gieder et al. 2014. Laczo et al. 2014, U.S. Army Corps of Engineers 2014).

Our hindcasted and forecasted modeling results relating near-shore sand deposition to decreased nesting habitat availability for Piping Plovers are consistent with field studies which demonstrated that beach nourishment, usually in concert with other human modifications such as un-notched berm or jetty construction, precedes a decrease in nesting habitat (Cohen et al. 2009; Schupp et al. 2013). Our findings of a decrease in the proportion of nesting habitat on the North End from 1999 to 2008 after the construction of an un-notched artificial foredune and biannual nearshore sand placement further allude to potential negative effects of some beach management strategies.

We caution that our forecasts showing an increase in the proportion of future suitable nesting habitat under modest sea-level rise rates and beach nourishment should be interpreted in the context of known, past negative impacts of beach nourishment on piping plover habitat suitability. Negative effects on nesting habitat suitability in the short term could affect the ability of future piping plover populations to respond to increased habitat suitability due to SLR in the long-term. Thus, an increase in future long-term habitat suitability may not yield benefits on a population-level if short-term effects of beach management have negative population consequences.

Our findings provide an important starting point for further developing and testing of this tool that can be used to predict how Piping Plover nest habitat will change with proposed efforts to use beach nourishment as part of a suite of human modifications planned in response to threats of SLR or tropical storm events (see U.S. Fish and Wildlife Service 2009 for a review of existing or proposed inlet and shoreline stabilization projects). While we did model the future effects of SLR in combination with biannual near-shore sand placement and a heavily notched foredune, we must also model the effects of on-shore sand placement and un-notched foredune, and caution that our current results cannot be used to make inferences about those or other potential beach management activities until predictions are further verified with both short-term and long-term data from specific scenarios and island sites. Further analyses of the geomorphology output under varying scenarios of sand placement, foredune height, and notch creation should be informative to managers considering the use of these strategies for storm protection and would show the implications of proposed approaches for nesting Piping Plovers. It is important to reiterate that while we showed no differences in future conditions with or without a heavily-notched foredune (i.e. 30% of foredune notched and open to overwash), due to the accumulated geomorphological effects of 3-4.1 mm/yr SLR over 50-100 years, we cannot make predictions about shorter-term changes under this current modeling framework. We know from hindcasting, that over a short-time period, sand deposition and an un-notched foredune led to declining habitat suitability, thus without the cumulative effects of 50-100 years of SLR, we should assume the same short-term decline in habitat suitability would be observed.

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Chapter 5: Summary of peer-reviewed publications and presentations related to work products.

Peer-Reviewed Publications

Gieder, K., Karpanty, S.M., Fraser, J.D., Catlin, D.H., Gutierrez, B.T., Plant, N.G., Turecek, A.M., and Thieler, E.R. 2014. A Bayesian network approach to predicting nest presence of the federally-threatened piping plover using barrier island features. *Ecological Modeling* 276: 38-50.

Gieder, K., Gutierrez, B.T., Karpanty, S.M., Plant, N.G., Thieler, E.R., Fraser, J.D., and Catlin, D.H. In preparation to be submitted 2015. Quantifying the cascading effects of sea-level rise and management decisions on barrier island geomorphology and nesting habitat of the federally-threatened Piping Plover (*Charadrius melodus*). *PLoS ONE*.

Gutierrez, B., Plant, N., Thieler, E., and Turecek, A. In revision. Using a Bayesian network to predict barrier island geomorphological characteristics. *Journal of Geophysical Research*.

Presentations at Scientific or Management Meetings

2014	Gieder, K., Karpanty, S.M., Gutierrez, B., Thieler, E., Plant, N., Fraser, J.D., and Catlin, D. Assessing the impacts of sea level rise on piping plovers at Assateague Island. Atlantic Coast Piping Plover and Least Tern Workshop, Shepherdstown, West Virginia. February 2014.
2014	Gutierrez, B., Gieder, K., Karpanty, S.M., Thieler, E.R., and Plant, N. Using Bayesian networks to predict coastal vulnerability to sea level rise. USGS Climate Change in Urban Settings Workshop, Baltimore, Maryland, February 2014.
2014	Thieler, E., Gutierrez, B., Plant, N., Karpanty, S.M., Gieder, K. Evaluating the risks and uncertainties in barrier island responses to climate change. Northeast Climate Change Center Webinar, Boston, Massachusetts, February 2014.
2013	Karpanty, S.M. Effects of sea-level rise on piping plover habitat along the U.S. Atlantic Coast. Virginia Coast Reserve LTER Annual Meeting, May,Oyster, Virginia.
2013	Karpanty, S., Gieder, K., Gutierrez, B. Effects of sea-level rise and altered storminess on Piping Plover (<i>Charadrius melodus</i>) habitat along the U.S. Atlantic Coast." Nonbreeding Piping Plover Conservation Workshop. 14-16 January 2013. Beaufort, SC.

2012	Gieder, K., Karpanty, S., Fraser, J. and Catlin, D. Effects of sea-level rise and altered storminess on Piping Plover (<i>Charadrius melodus</i>) habitat along the U.S. Atlantic Coast." Virginia Tech GIS and Remote Sensing 2012 Research Symposium, 13 April 2012, Blacksburg, Virginia. Poster Presentation.
2012	Gieder, K., Karpanty, S., Fraser, J. and Catlin, D. Effects of sea-level rise and altered storminess on Piping Plover (<i>Charadrius melodus</i>) habitat along the U.S. Atlantic Coast. Virginia Coastal Avian Partnership Annual Meeting, April 2012, Melfa, Virginia.
2012	Gieder, K., Karpanty, S.M., Fraser, J.D. and Catlin, D.H. Historical data on piping plover responses to storms and construction of a storm berm at Assateague Island National Seashore provides basis for modeling effects of future sea-level rise and altered storminess. 125 th Wilson Ornithological Conference, 7-10 March 2013, Williamsburg, Virginia.
2012	Thieler, R., and Karpanty, S.M. Forecasting effects of accelerating sea- level rise on the habitat of Atlantic Coast piping plovers and identifying responsive conservation strategies. U.S. Regional Association for the International Association for Landscape Ecology, 8-12 April 2012, Newport, Rhode Island. Poster presentation.
2012	Karpanty, S.M. Effects of sea-level rise on piping plover habitat along the U.S. Atlantic Coast. Virginia Tech GIS and Remote Sensing 2012 Research Symposium, 13 April 2012, Blacksburg, Virginia.
2012	Karpanty, S.M. Effects of sea-level rise on piping plover habitat along the U.S. Atlantic Coast. U.S. Fish and Wildlife Service's Northeast Region's Science Seminar Series, 26 January 2012, Hadley, MA.
2012	Karpanty, S.M., Gieder, K., Catlin, D., and Fraser, J.D. Effects of sea- level rise on piping plover habitat along the U.S. Atlantic Coast. 2012 Biannual Piping Plover and Least Tern Workshop. National Conservation Training Center, 18-20 January 2012, Shepherdstown, West Virginia.
2011	Gieder, K., Karpanty, S.M., Fraser, J. and Catlin, D. Effects of sea level rise and altered storminess on Piping Plover habitats along the U.S. Atlantic and Gulf Coasts. The Waterbird Society 35th Annual Meeting, 9- 12 November, Annapolis, Maryland. Poster presentation.
2011	Karpanty, S.M., Gieder, K., Thieler, R., Plant, N., and Gutierrez, B. Forecasting effects of accelerating sea-level rise on the habitat of Atlantic Coast piping plovers and identifying responsive conservation strategies. Northeast Regional Conservation Needs and Landscape Conservation

	Cooperatives Partners Meeting, 4 th June 1, Albany, NY. Poster presentation.
2010	Karpanty, S.M., Catlin, D., Fraser, J.D., and Cohen, J. Incorporating piping plover habitat ecology into a sea-level rise decision support model. Sea-level rise hazards and decision support meeting. National Conservation Training Center, 13 October 2010, Shepherdstown, West Virginia.
2010	Gutierrez, B., Karpanty,S.M., Gieder, K. Assessing the impacts of sea level rise and climate change on piping plovers. Piping Plover Wintering Conservation Workshop, January, Fernandina Beach, FL.

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