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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

Many shorebird species are threatened by the impacts of sea-level 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 km^2 (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 (MacIvor, 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 sea-level 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

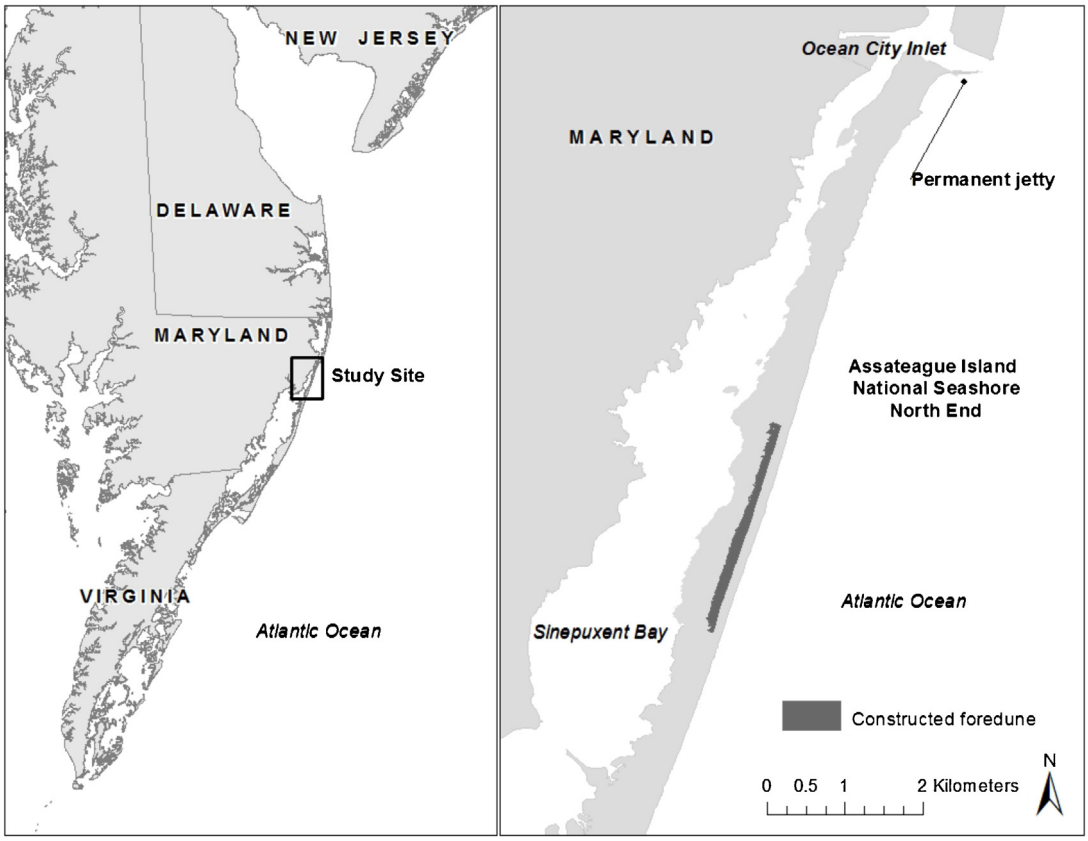

Fig. 1. We used piping plover (*Charadrius melodus*) nest locations and random points without nests, and data on physical features, from the northern 10 km of Assateague Island National Seashore, MD, USA, to construct a Bayesian network to predict the probability of nest presence and absence. A human 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 bi-annual 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 m^3 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, bi-annually replenishing approximately 144,000 m^3 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

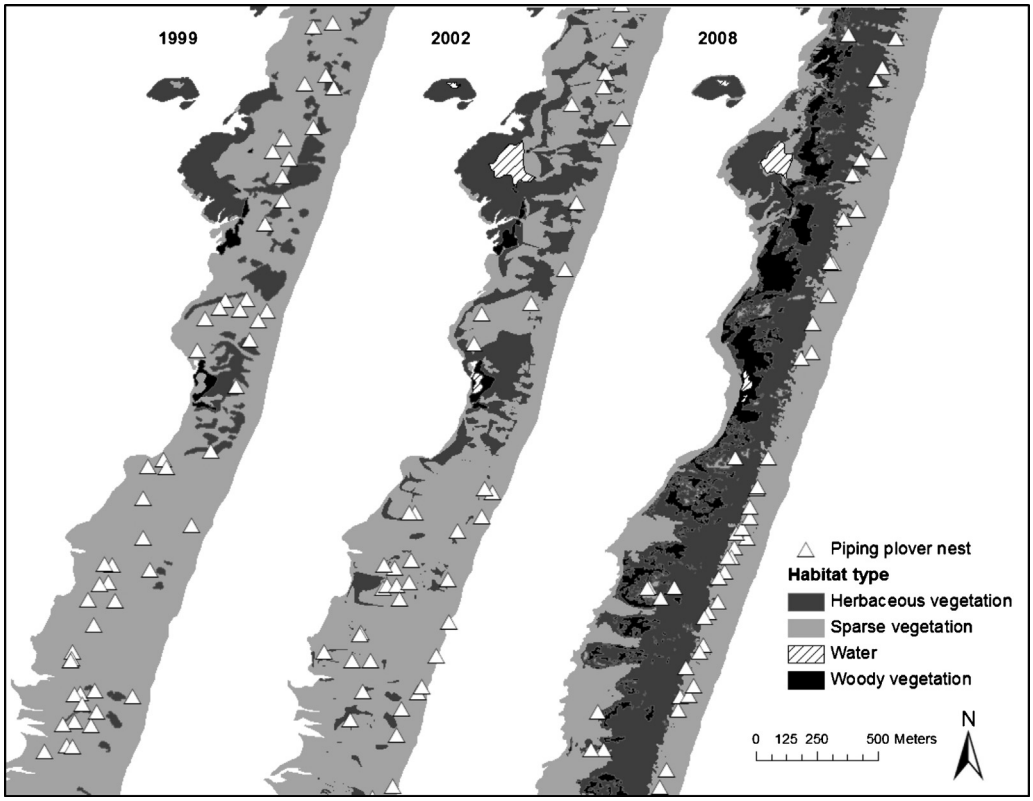

Fig. 2. Distribution of piping plover (*Charadrius melodus*) nests and vegetation types (sparse, herbaceous, woody) recorded by National Park Service staff in their habitat maps in 1999 (a), 2002 (b), and 2008 (c) on the North End of Assateague Island National Seashore, MD, USA. The Atlantic Ocean is 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 to 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

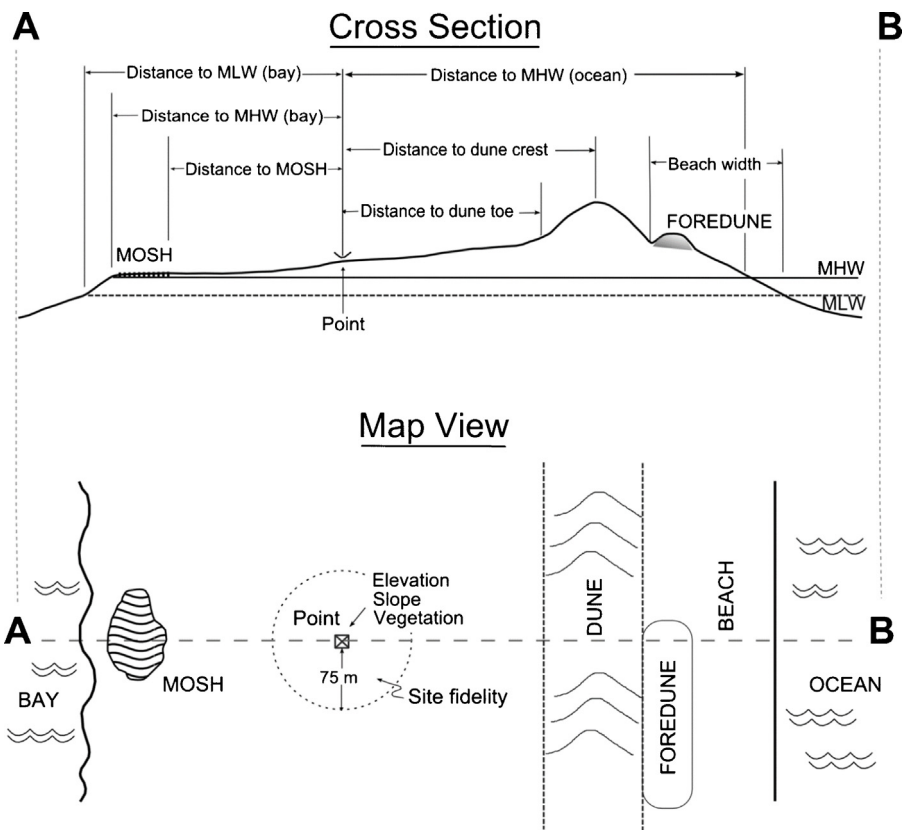

Fig. 3. Conceptual diagram illustrating the features we used to define the 12 physical and site fidelity variables in our Bayesian network, including the distances to features. MHW and MLW are the mean high water and mean low water boundaries, respectively. All distances, beach widths, and point elevations 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

Table 1
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 low water bay boundary to the nest or random point without nest, "Distance to MOSH (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 from the preceding year, "Slope (%)" is the average rise over run within 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:

$$P(X_1 \ldots X_n) = \prod_i P(X_i \; Pa(X_i))$$

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.

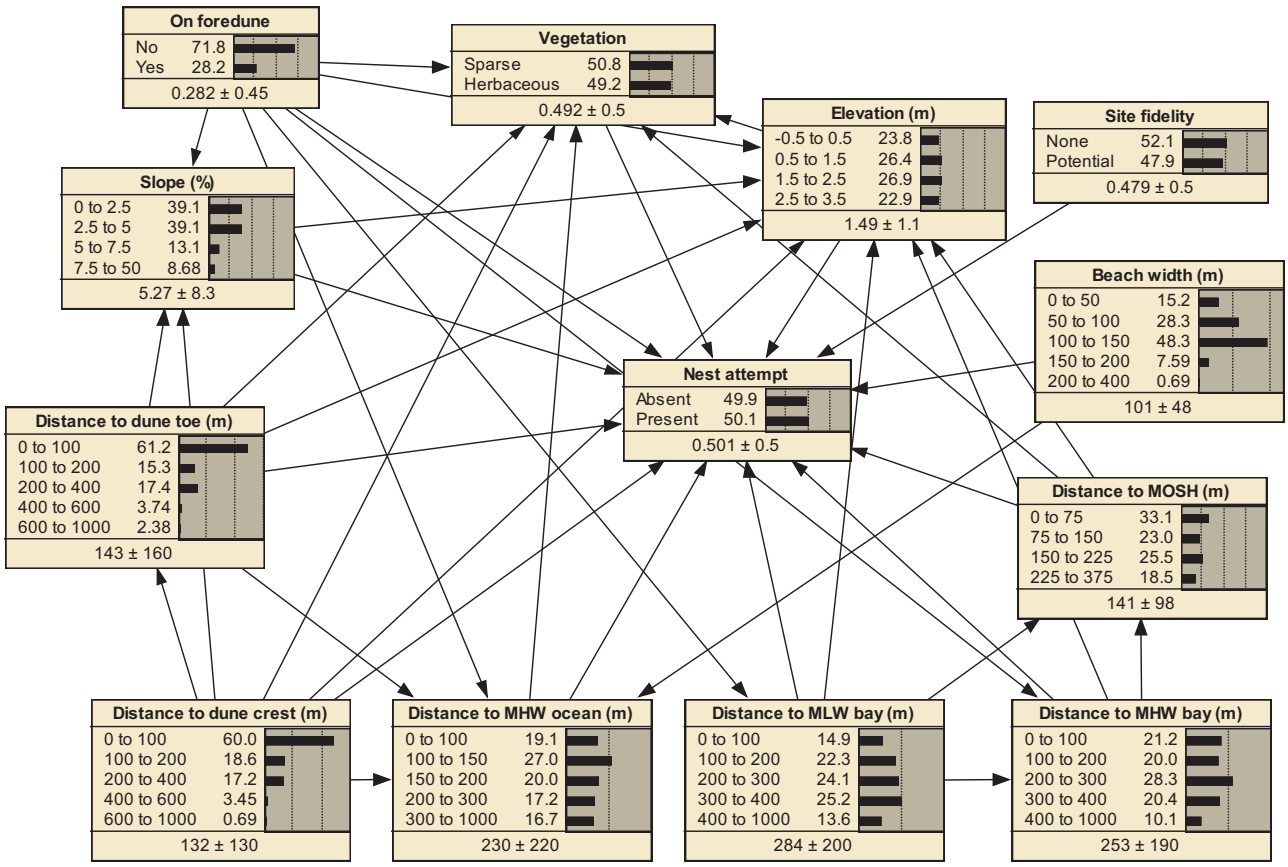

Fig. 4. Bayesian network showing probabilities of piping plover (*Charadrius melodus*) nest presence (50.1%) and absence (49.9%) conditioned on 2008 data from all 12 physical and site fidelity variables from Assateague Island National Seashore, MD, USA; constructed using Netica BN software (Norsys, 1992–2010). 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 $\mu = \Sigma_x x\,p(x)$.

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 actual data for each model compared to the likelihood of the uninformed priors for those models. We calculated a percentage change for each model that represented the change in the $LR_{predict}$ from the LR_{actual}:

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

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 impossible because the prediction would have to fit the model better than 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

Table 2
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

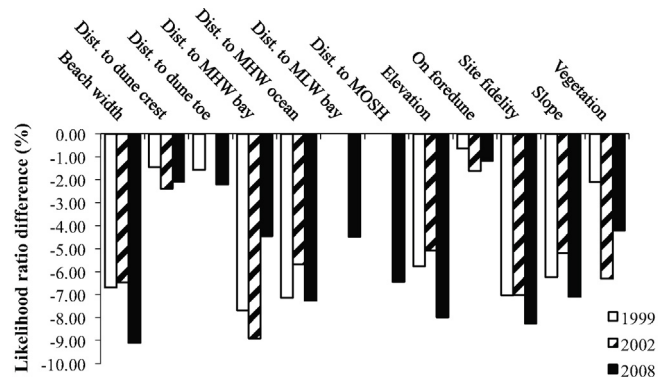

Fig. 5. Likelihood ratio difference (%) for 12 piping plover (*Charadrius melodus*) nest presence variables in 1999, 2002, and 2008 at Assateague Island National Seashore, MD, USA. Likelihood ratio difference represents the difference from the likelihood of the model predictions given data from all 12 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.

Table 3
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 low water bay boundary to the nest or random point without nest, "Distance to MOSH (m)" (MOSH) 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, "Site 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, "Vegetation" is the general type and density of vegetation at 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 ± 0.2 m; mean ± SE) than the average elevation of nests in the rest of the study area (1.0 ± 0.4 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

Table 4
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 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 low water bay boundary to the nest or random point without nest, "Distance to MOSH (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 from the preceding year, "Slope (%)" is the average rise over run within 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] "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 km^2) 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 sea-level 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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