ASSESSING THE EFFECTS OF SEA-LEVEL RISE ON PIPING PLOVER (*CHARADRIUS MELODUS*) NESTING HABITAT, AND THE ECOLOGY OF A KEY MAMMALIAN SHOREBIRD PREDATOR, ON ASSATEAGUE ISLAND

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ABSTRACT

The piping plover (*Charadrius melodus*) is a federally-listed shorebird that nests on barrier islands along the U.S. Atlantic Coast and is highly vulnerable to habitat change and predation. We have addressed these two threats by 1) developing and implementing a linked model system that predicts future change to piping plover habitat resulting from sea-level rise and beach management efforts by joining dynamic models of sea-level rise, shoreline change, island geomorphology and piping plover nest habitat suitability, and 2) quantifying occupancy and movement of the red fox (*Vulpes vulpes*), a key shorebird predator at Assateague Island, Maryland and Virginia. We constructed and tested a model that links changes in geomorphological characteristics to piping plover nesting habitat suitability. We then linked this model to larger scale shoreline change resulting from sea level rise and storms. Using this linked model to forecast future sea-level rise and beach management efforts, we found that modest sea-level rise rates (3 mm and 4.1 mm/yr; similar to current rates) may increase suitable piping plover nesting habitat area in 50–100 years and some beach management strategies (beach nourishment and artificial dune modifications) also influence habitat availability. Our development and implementation of this tool to predict change in piping plover habitat suitability provides a vital starting point for predicting how plover nesting habitat will change in a context of planned human modifications intended to address climate change-related threats. Our findings regarding red fox occupancy and movement complement the use of this model for planning future management actions by providing vital information on the effects of certain predator management activities and habitat use of a key mammalian predator, the red fox, for shorebirds along the U.S. Atlantic Coast. Overall, we found that 1) red fox occupancy was strongly tied to eastern cottontail (*Sylvilagus floridanus*) trap success, increasing sharply with increased eastern cottontail trap success, 2) red fox occupancy did not change in response to an intensive eradication program, and 3) red foxes in our study area generally moved little between camera stations spaced 300 m from each other, but may move large distances (> 6km) at times, likely to occupy new territory available after lethal control efforts. Our findings have important ramifications for the sustainability of long-term predator removal programs and our understanding of future habitat change on the red fox. For example how vegetation changes affect eastern cottontails, how resulting fluctuations in eastern cottontails affect red fox occupancy, and how consequential changes in red fox occupancy affect plover breeding productivity. Our predictive model combined with these predator findings will allow wildlife managers to better plan and implement effective management actions for piping plovers in response to the multiple stressors of SLR-induced habitat change and predation.

Dedicated to

Barbara Anne Boudreau

My inspiration for everything and my biggest supporter who passed on her incredible strength, determination, and passion for life that made this all possible.

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Attribution

A brief description of the contributions made by my colleagues that assisted with the preparation of my dissertation chapters is outlined below. Contributions rose to the level of co-author for manuscript publication for four of my chapters.

Chapter 2: A Bayesian Network Approach to Predicting Nest Presence of the Federally-threatened Piping Plover (*Charadrius melodus*) using Barrier Island Features

Authors: Gieder K. D., Karpanty S. M., Fraser J. D., Catlin D. H., Gutierrez B. T., Plant N. G., Turecek A. M., Thieler E. R.

Sarah Karpanty (Department of Fish & Wildlife Conservation, Virginia Tech) provided study design, financial, logistic, and statistical assistance and provided edits of the manuscript. Jim Fraser and Dan Catlin (Department of Fish & Wildlife Conservation, Virginia Tech) provided assistance with study design and edits to manuscript. Benjamin Gutierrez and Nathaniel Plant (US Geological Survey) completed statistical analyses and modeling, provided assistance with data collection, study design, and edits to manuscript. Aaron Turecek (US Geological Survey) provided assistance with data analyses and collection. Rob Thieler (US Geological Survey) provided edits to manuscript.

Chapter 3: Forecasting the effects of sea-level rise and anthropogenic beach modification on threatened piping plover (*Charadrius melodus*) nesting habitat

Authors: Gieder K. D., Gutierrez B. T., Karpanty S. M., Plant N. G., Thieler E. R., Fraser J. D., Catlin D. H.

Benjamin Gutierrez (US Geological Survey) provided assistance with data collection, study design, and edits to manuscript. Sarah Karpanty (Department of Fish & Wildlife Conservation, Virginia Tech) provided study design, financial, logistic, and statistical assistance and provided edits of the manuscript. Nathaniel Plant and Rob Thieler (US Geological Survey) provided assistance with study design and edits to manuscript. Jim Fraser and Dan Catlin (Department of Fish & Wildlife Conservation, Virginia Tech) provided assistance with study design and edits to the manuscript.

Chapter 4: Red fox (*Vulpes vulpes*) occupancy and habitat use on Assateague Island National Seashore, Maryland

Authors: Gieder K. D., Karpanty S. M., Kumer J., Hulslander B., Fraser J. D., Catlin D. H.

Sarah Karpanty (Department of Fish & Wildlife Conservation, Virginia Tech) provided study design, financial, logistic, and statistical assistance and provided edits of the manuscript. Jim Fraser and Dan Catlin (Department of Fish & Wildlife Conservation, Virginia Tech) provided assistance with study design and edits to the manuscript. Jack Kumer and Bill Hulslander (Assateague Island National Seashore) provided assistance with data collection and study design.

Chapter 5. Red fox (*Vulpes vulpes*) movement on Assateague Island National Seashore, Maryland

Gieder K. D., Karpanty S. M., Kumer J., Hulslander B., Fraser J. D., Catlin D. H.

Sarah Karpanty (Department of Fish & Wildlife Conservation, Virginia Tech) provided study design, financial, logistic, and statistical assistance and provided edits of the manuscript. Jim Fraser and Dan Catlin (Department of Fish & Wildlife Conservation, Virginia Tech) provided assistance with study design and edits to the manuscript. Jack Kumer and Bill Hulslander (Assateague Island National Seashore) provided assistance with data collection and study design.

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Chapter 1

ASSESSING THE EFFECTS OF SEA-LEVEL RISE ON PIPING PLOVER (*CHARADRIUS MELODUS*) NESTING HABITAT, AND THE ECOLOGY OF A KEY MAMMALIAN SHOREBIRD PREDATOR, ON ASSATEAGUE ISLAND

Introduction

The piping plover *(Charadrius melodus)* is a small inconspicuous shorebird that was federally-listed under the Endangered Species Act by the U.S. Fish and Wildlife Service (USFWS) in 1986 (USFWS 1985). Piping plovers are listed as federally-threatened where they breed along the U.S. Atlantic coast and share this habitat with an array of other imperiled species including American Oystercatchers *(Haematopus palliatus)*, Wilson's Plovers *(Charadrius wilsonia),* Least Terns *(Sternula antillarum)*, Common Terns *(Sterna hirundo)*, Gull-billed Terns *(Gelochelidon nilotica),* Roseate Terns *(Sterna dougallii),* Black Skimmers *(Rynchops niger),* Puritan tiger beetles *(Cicindela puritana),* Loggerhead *(Caretta caretta)* and Green *(Chelonia mydas)* sea turtles, and Seabeach Amaranth *(Amaranthus pumilus*; USFWS 1996). Federal- and/or state-management actions designed to conserve and protect the large extent of coastal habitat that Atlantic coast piping plovers occupy consequently benefit many other species that depend on this same habitat.

Declines in piping plovers have been well documented and have been attributed to a number of different causal factors through time, including hunting in the early 1900s (Bent 1929), and coastal development and human disturbance post World War II (Hecker 2008). The most recent recovery plan for the Atlantic Coast piping plover population lists habitat loss and degradation from human development and sea-level rise (SLR), disturbance from humans and pets, and predation as major factors challenging the recovery of this species (USFWS 1996). In my dissertation, I aim to provide new knowledge concerning the threats of SLR and predation to facilitate effective management of piping plovers on the U.S. Atlantic Coast. I introduce these threats briefly here, then outline the chapters of my dissertation which each address components of these challenges in more details

Effects of sea-level rise on piping plovers

Human development is a major driver of habitat loss for piping plovers across their range (USFWS 2009). Piping plovers along the U.S. Atlantic Coast face an added threat of potential habitat loss or change from sea-level rise (SLR), along with beach management strategies that attempt to stabilize or mitigate the changes resulting from SLR. Piping plovers nest on low elevation beaches and barrier islands along the Atlantic Coast and are known to respond rapidly to physical changes in their environment (Cohen et al. 2009, Kumer 2004, Schupp et al. 2013). Thus, piping plovers are an ideal species to model SLR and beach management effects on barrier island habitat and shorebirds, as has been done in previous studies (Aiello-Lammens et al. 2011, Seavey et al. 2011). However, there has been little work done to explicitly link how SLR 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 SLR effects; 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). Previous studies investigating SLR effects on wildlife species did not explicitly link what was known about plover habitat preferences to relative rates of SLR and storm-driven changes in dynamic barrier island morphology. Instead, past efforts assumed an average historic SLR rate, static geomorphology, or modeled dynamic response using simplified beach or barrier island geometries (Seavey et al. 2011, Benscoter et al. 2013, Reece et al. 2013a, b, Sims et al.

2013, Gieder et al. 2014). Though these studies furthered our understanding of how SLR may affect barrier island wildlife habitat, we sought to develop a modeling framework that improves our ability to predict specific barrier island geometries under future SLR, storm, and management scenarios and to evaluate future plover habitat suitability.

Effects of predators on piping plovers

The challenges of managing dynamic habitats for piping plover conservation in the face of sea-level rise are further exacerbated by a lack of knowledge regarding another major threat to recovery, namely shorebird predators. Mammalian mesopredators such as red fox (*Vulpes vulpes*), raccoon (*Procyon lotor*), striped skunks (*Mephitis mephitis*), and Virginia opossums (*Didelphis virginiana*) have been implicated in reduced productivity for shorebirds, including piping plovers (Hecht and Nickerson 1999, Kruse et al. 2001, Cohen et al. 2009). Though shorebirds have evolved many defense mechanisms against predators (Gochfeld 1984), a suspected increase in shorebird nest and chick predation, combined with other increasing threats such as habitat loss and disturbance, have made predator management a key part of recovery plans for imperiled shorebird species (USFWS 1996, Schulte et al. 2007, Cohen et al. 2009, USFWS 2013).

However, the effectiveness of many predator control programs is questioned because predator effects on piping plovers and predator ecology on the U.S. Atlantic coast are poorly understood. One factor behind our lack of knowledge is that human expansion and development have altered the habitat along our coasts such that it is increasingly suitable for many predator species, thereby changing their historic distributions and habitat use, while also changing habitat suitability for nesting shorebirds (Evans 2004, Scott et al. 2014). Current predator management techniques, such as predator exclosures, electric fencing, and lethal removal in coastal habitats are largely informed by trial and error methods, with little prior knowledge of site-specific predator behavior and habitat use patterns. In addition, little is understood about shorebird predators, particularly concerning aspects of their population ecology such as factors affecting presence and absence, and how they move across the barrier island landscape.

The importance of understanding SLR and predators to best manage piping plovers

Understanding future effects of SLR and the ecology of a major predator, the red fox, will provide useful information for beach managers. The high profile status of piping plovers as a species of conservation concern has resulted in increasing costs over the past few decades for coastal habitat restoration and plover protection. For example, in 1993, an estimated $2.28 million was spent protecting piping plover breeding habitat along the U.S. Atlantic Coast. The cost increased to $3.44 million in 2002 (Hecht and Melvin 2009). The latest 5-year review by the USFWS outlining goals, measures, and actions for piping plover conservation estimated expected annual costs for these activities to total $3.63 million per year along the Atlantic coast breeding areas alone, and $539, 260 in their Atlantic Coast wintering range (USFWS 1996).

The economic and ecological importance of effective piping plover management cannot be understated. Unfortunately, current and future planned habitat and predator management efforts are hindered by our inabilities to adequately predict future coastal changes and to understand how predators use current and future barrier island habitats. Both the environmental and economic implications of continuing to manage coastal habitats and predators without incorporating an understanding of SLR and beach management effects, and knowledge of the predators' ecology, underscore the need to address these deficiencies.

Dissertation goals and objectives:

My ultimate goals were to 1) develop and implement a tool to predict future change to piping plover habitat resulting from sea-level rise and beach management efforts, and 2) address gaps in our understanding of shorebird mammalian predator population ecology, in particular red fox which are a predator of management concern on Assateague Island and elsewhere on the Atlantic Coast. In combination, the new information on the key threats of habitat change and predators presented in my work will allow wildlife managers to better plan and implement effective management actions for piping plovers in response to the multiple stressors of SLR-induced habitat change and predation. The following four chapters of my dissertation, including detailed objectives and relation to my overarching goals, are described briefly below.

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

Published in Ecological Modelling (Gieder et al. 2014).

Authors: Gieder K. D., Karpanty S. M., Fraser J. D., Catlin D. H., Gutierrez B. T., Plant N. G., Turecek A. M., Thieler E. R.

Objectives:

- Use remote sensing and field data collected in 1999, 2002, and 2008 from Assateague Island, MD and VA to develop a model that links piping plover (*Charadrius melodus*) nesting habitat suitability to physical features of their nesting habitat.
- Use this model to develop habitat suitability probabilities on Assateague Island for those past three years.
- Test these predicted probabilities against actual nests and random points from those three years so that the utility of the model for forecasting can be assessed.

II. Forecasting the effects of sea-level rise and anthropogenic beach modification on threatened piping plover (*Charadrius melodus*) nesting habitat

To be submitted to PLOS ONE August 2015.

Authors: Gieder K. D., Gutierrez B. T., Karpanty S. M., Plant N. G., Thieler E. R., Fraser J. D., Catlin D. H.

Objectives:

- Develop three linked models (shoreline change, geomorphology, piping plover (*Charadrius melodus*) habitat suitability) that integrate processes on different spatial and temporal scales, and forecast change in piping plover nesting habitat on Assateague Island, MD and VA as a function of dynamic barrier island response to sea-level rise and beach management efforts.
- Test hindcasting nesting habitat suitability probabilities from 1999, 2002, and 2008 against actual nests in these years and evaluate model sensitivity by testing individual model variables for accuracy at different stages of the linking process.
- Use this linked model to forecast the effects of various sea-level rise rates and beach nourishment effects on piping plover nesting habitat in the next 50-100 years at Assateague Island.

III. Red fox (*Vulpes vulpes*) occupancy and habitat use on Assateague Island, Maryland, USA

To be submitted to Journal of Mammalogy September 2015.

Authors: Gieder K. D., Karpanty S. M., Kumer, J., Hulslander, B., Fraser, J. D., Catlin, D. H.

Objectives:

- Photographically sample red fox (*Vulpes vulpes*) across three camera grids on Assateague Island, MD, covering a range of barrier island habitats.
- Estimate occupancy and detection for red fox across the landscape.
- Identify the effects of habitat type, co-occurring carnivore species, prey species, ungulate species, and human presence on red fox occupancy.
- Investigate how targeted eradication efforts in one of the camera grids affects red fox occupancy and detection, and compare these effects to occupancy and detection in the other camera grids with no eradication efforts, in order to make future recommendations about best predator management practices to benefit shorebirds.

IV. Red fox (*Vulpes vulpes*) movement on Assateague Island, Maryland, USA

To be submitted to Journal of Coastal Conservation September 2015

Authors: Gieder K. D., Karpanty S. M., Kumer, J., Hulslander, B., Fraser, J. D., Catlin, D. H.

Objectives:

- Photographically sample red fox (*Vulpes vulpes*) across three camera grids on Assateague Island, MD, covering a range of barrier island habitats.
- Identify individual red foxes from photographs using unique plumage coloration and patterning, and scars.
- Use the locations of camera stations where these individuals were seen to identify potential seasonal, spatial, and sexual differences in fox movement.
- Assess how this knowledge of individual fox movement may be used to best design future monitoring and management efforts.

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CHAPTER 2

A BAYESIAN NETWORK APPROACH TO PREDICTING NEST PRESENCE OF THE FEDERALLY-THREATENED PIPING PLOVER (*CHARADRIUS MELODUS*) USING BARRIER ISLAND FEATURES

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 modelling 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 modelling 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.

Keywords: Bayesian network, development, habitat, piping plover, sea-level rise, shorebird

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 Jr. and FitzGerald, 2004). Along the U.S. 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 breeding habitat for many shorebird species, including the piping plover (*Charadrius melodus*), a shorebird that was federally listed as threatened along the U.S. Atlantic Coast under the U.S. Endangered Species Act in 1986 (USFWS, 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 modelling 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), Maryland, 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.

Methods

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 (38o05' N, 75o12' W, Figure 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 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, 1996). 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 (Figure 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., 2013; Carruthers et al., 2011; Schupp et al., 2013; Schupp et al., 2007; Figure 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 portion 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 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 (Figure 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., 2009; Stockdon et al., 2007). 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., 2009; Stockdon et al., 2007). 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., 2005). 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 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. We included all MOSH polygons in the island interior and in the intertidal zone. 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., in prep).

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 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.

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., 2009; Cohen et al., 2008; Houghton, 2005; Maslo et al., 2011; Powell and Cuthbert, 1992). Next, we converted this diagram into a BN using Netica 4.16 (Figure 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; Figure 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:

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

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).

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.

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, '$\mathrm{LR}_{\mathrm{predict}}$') 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, '$\mathrm{LR}_{\mathrm{actual}}$'). In other words, $\mathrm{LR}_{\mathrm{predict}}$ indicated the likelihood of our model predictions compared to the likelihood of the uninformed priors for those models, whereas $\mathrm{LR}_{\mathrm{actual}}$ 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 $\mathrm{LR}_{\mathrm{predict}}$ from the $\mathrm{LR}_{\mathrm{actual}}$:

$$percentage\ change = \frac{LRpredict - LRactual}{|LRactual|} \times 100\%$$

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 percentage 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.

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.

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 1999–2008. 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 (Figure 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 towards 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.

Results

Model performance

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).

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 43–47% 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 $LR_{predict}$ 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).

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 (Figure 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 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).

Model Applications

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).

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 1999–2008. 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 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. −0.5–1.5 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).

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., 2009; Cohen et al., 2008; 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 Figure 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 to 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 to 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 (Figure 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.

Conclusions

This study represents an important step towards 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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Tables

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[b] (n)			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	–0.5–0.5	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

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[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 portion 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. 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.

	Error(%)[b]			Likelihood Ratio (LR)[c]		
Model[a]	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.

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

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[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.

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)	-0.5-0.5	-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

Figures

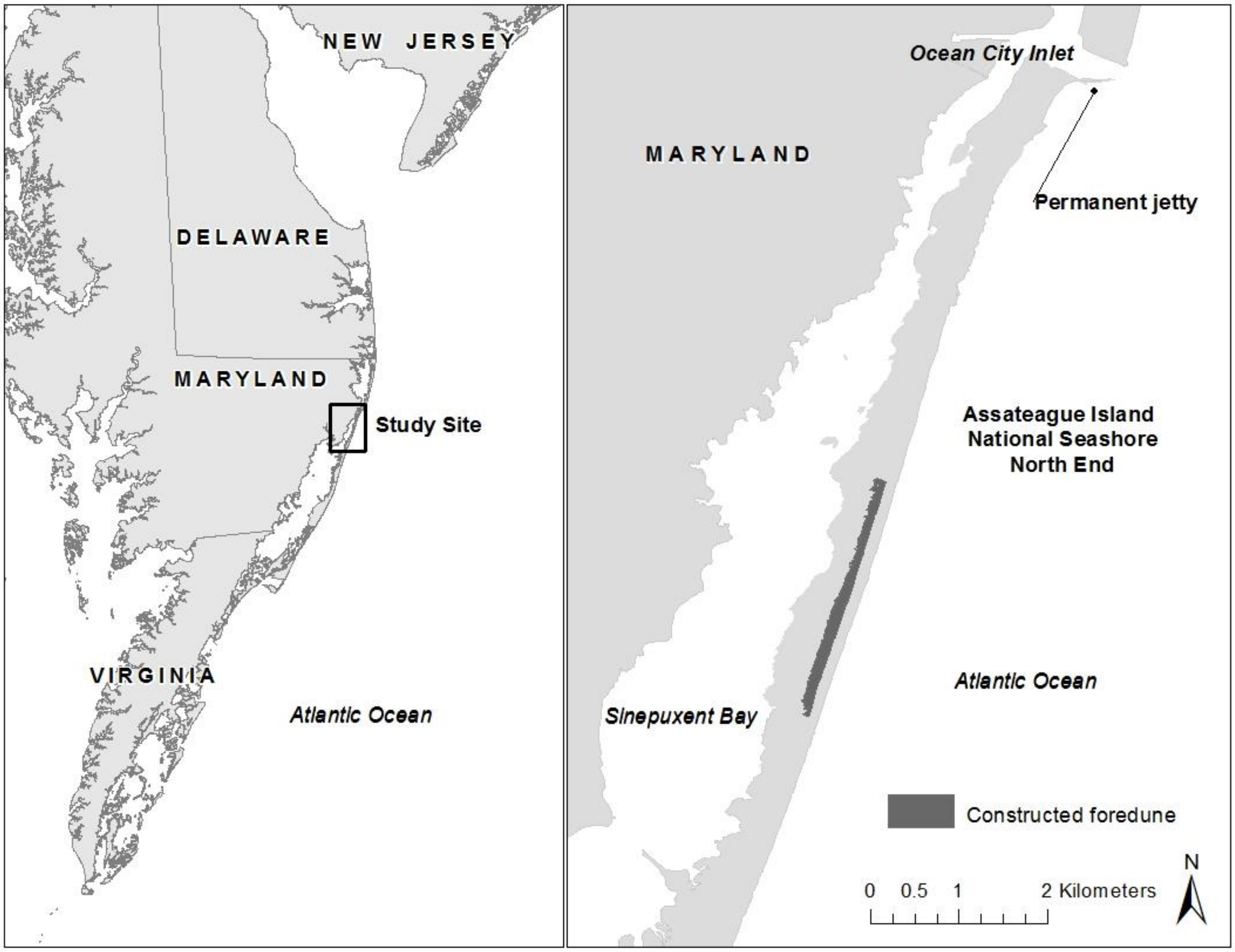

Figure 1. We used piping plover (*Charadrius melodus*) nest locations and random points without nests, and data on physical features, from the northern 10 km of Assateague Island National Seashore, MD, USA, to construct a Bayesian network to predict the probability of nest presence and absence. A human 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.

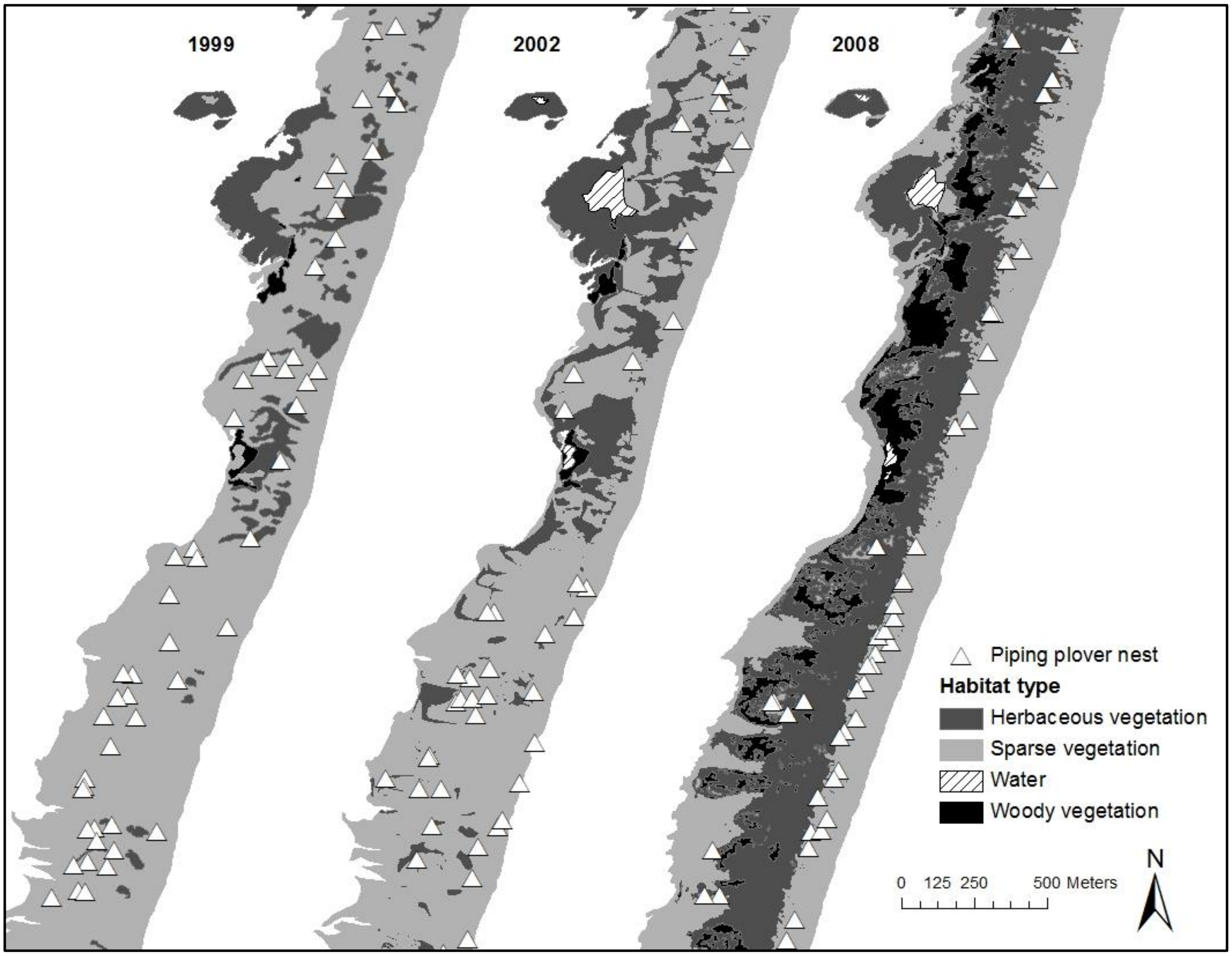

Figure 2. Distribution of piping plover (*Charadrius melodus*) nests and vegetation types (sparse, herbaceous, woody) recorded by National Park Service staff in their habitat maps in 1999 (a), 2002 (b), and 2008 (c) on the North End of Assateague Island National Seashore, MD, USA. The Atlantic Ocean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

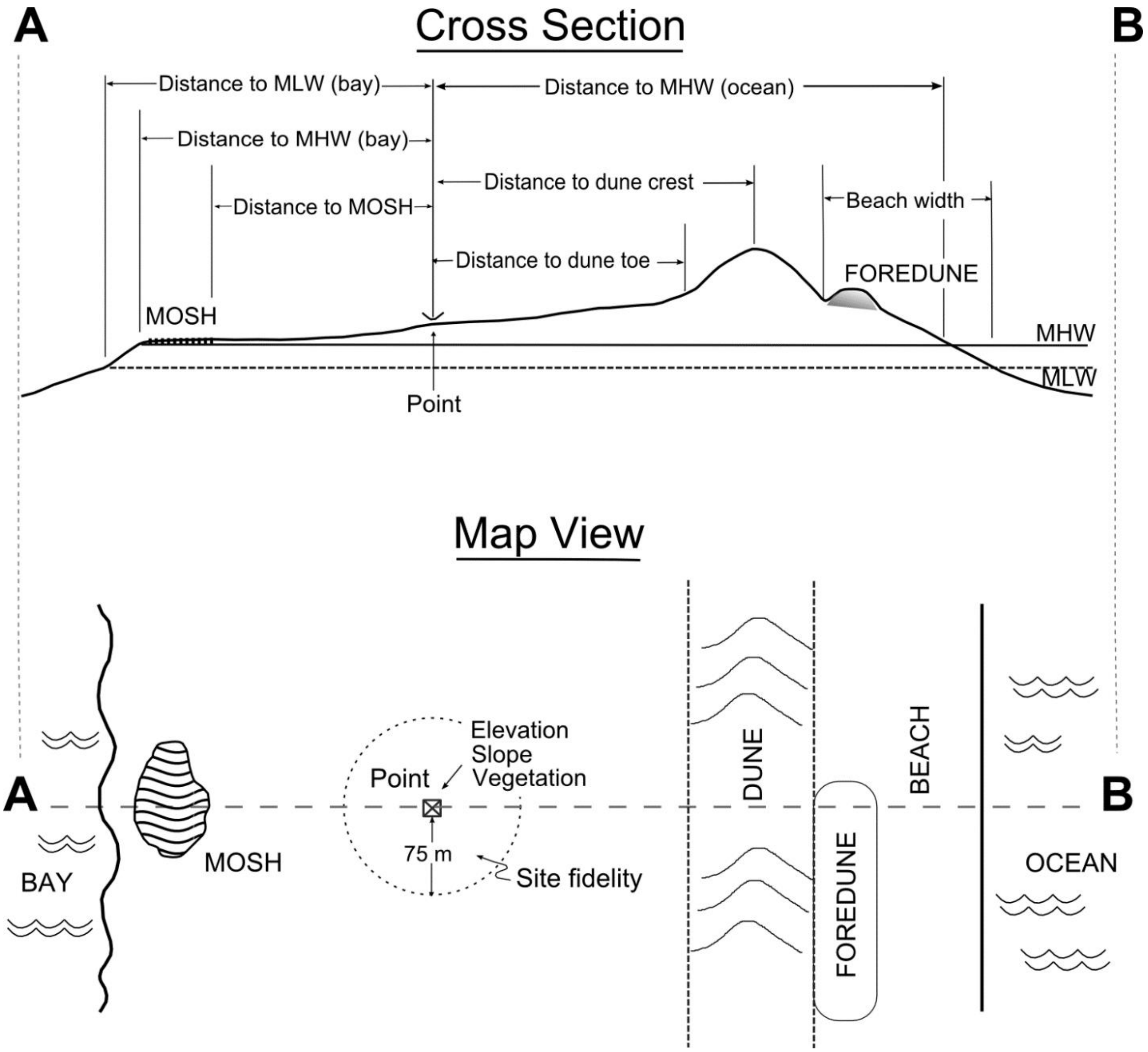

Figure 3. Conceptual diagram illustrating the features we used to define the 12 physical and site fidelity variables in our Bayesian network, including the distances to features. MHW and MLW are the mean high water and mean low water boundaries, respectively. All distances, beach widths, and point elevations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

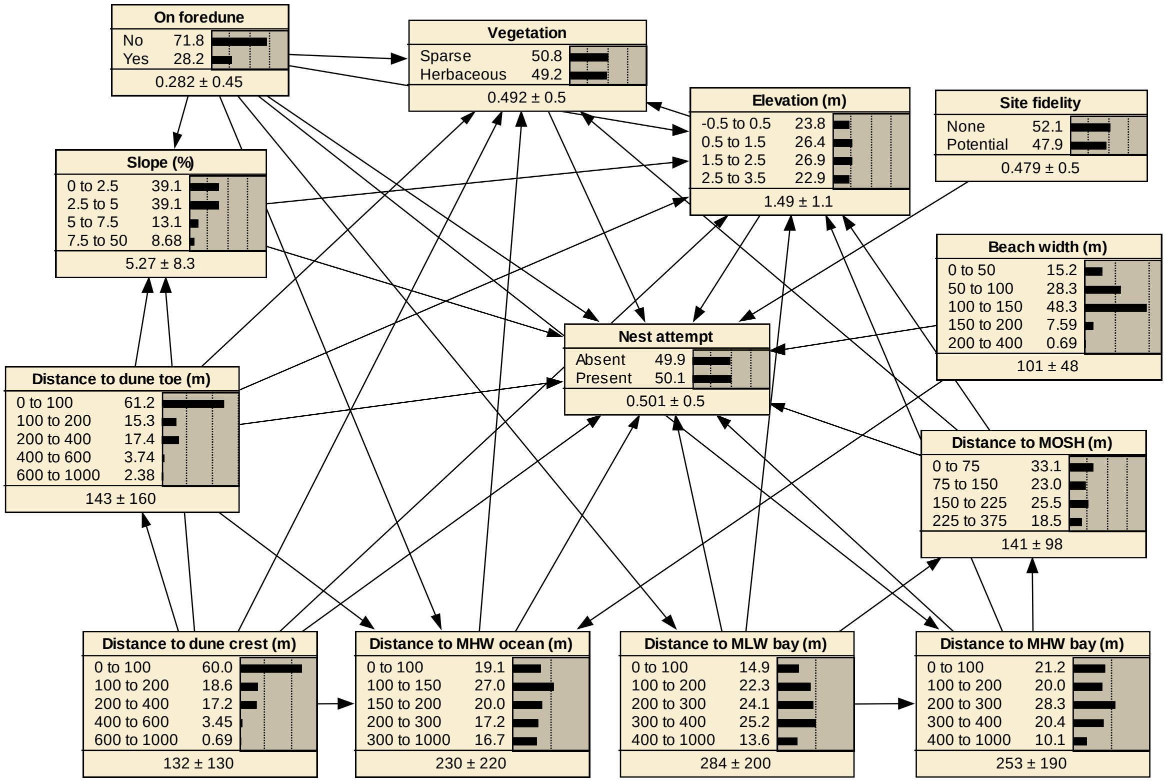

Figure 4. Bayesian network showing probabilities of piping plover (*Charadrius melodus*) nest presence (50.1%) and absence (49.9%) conditioned on 2008 data from all 12 physical and site fidelity variables from Assateague Island National Seashore, MD, USA; constructed using Netica BN software (Norsys,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

$\int_{-\infty}^{\infty} x\, p(x)\, dx$ and for discrete variables with assigned state values, the mean is represented by the equation $\mu = \sum_x x\, p(x)$.

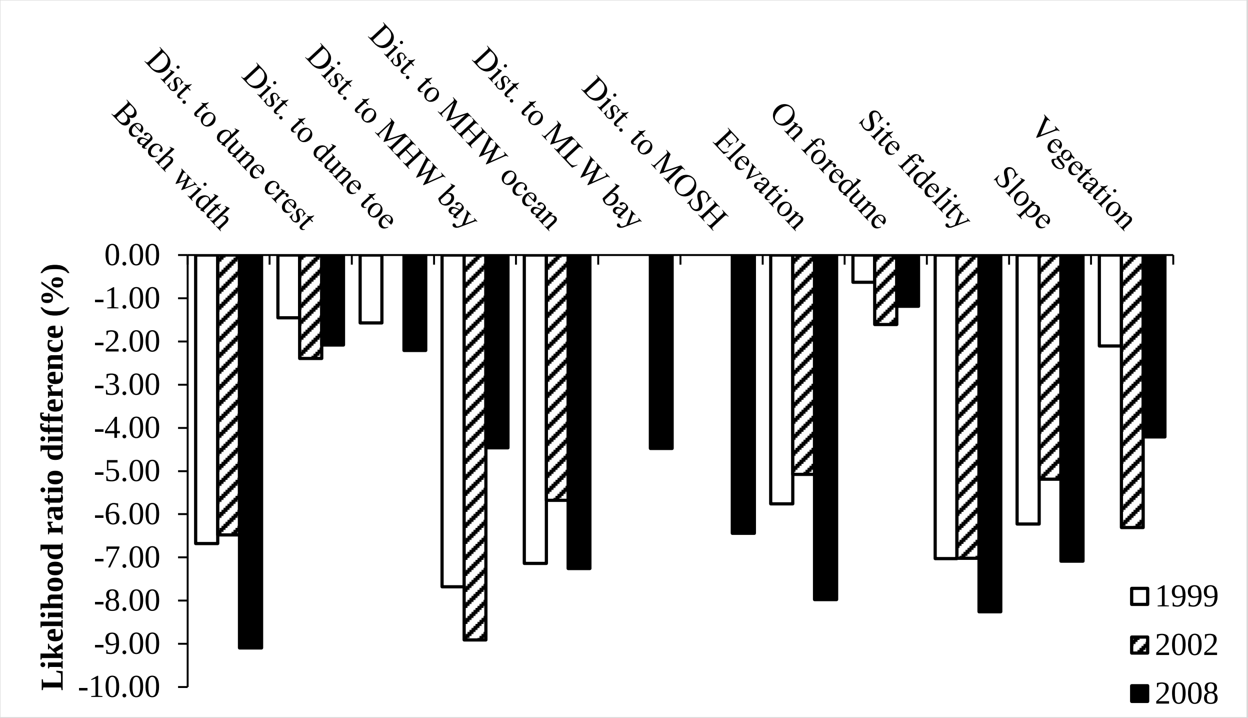

Figure 5. Likelihood ratio difference (%) for 12 piping plover (*Charadrius melodus*) nest presence variables in 1999, 2002, and 2008 at Assateague Island National Seashore, MD, USA. Likelihood ratio difference represents the difference from the likelihood of the model predictions given data from all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

CHAPTER 3

FORECASTING THE EFFECTS OF SEA-LEVEL RISE AND ANTHROPOGENIC BEACH MODIFICATION ON THREATENED PIPING PLOVER (*CHARADRIUS MELODUS*) NESTING HABITAT

Abstract

Barrier island habitats provide essential services for humans and support many wildlife species, including the federally-listed piping plover (*Charadrius melodus*). Barrier island morphology continually changes in response to storm activity over years to decades and to sea-level rise (SLR) over decades to millennia. Human efforts to maintain barrier island morphology, via beach nourishment or other management actions, influence the way these islands respond to storm activity and sea-level change. In the face of significant SLR projected for the next century, forecasts of barrier island changes that incorporate these factors have the potential to improve conservation of imperiled species like the piping plover. We have developed forecasts of changes in piping plover nesting habitat using three linked Bayesian Networks (BNs) that incorporate sensitivities to dynamic barrier island response. These BNs link probabilistic predictions of SLR impacts and storm effects on (1) shoreline change to (2) changes in barrier island geomorphology, including the effects of erosion management efforts, and finally to (3) changes in piping plover habitat suitability. Using datasets for Assateague Island in Maryland and Virginia in 1999, 2002, and 2008, we developed and tested the linked BNs to predict future changes in piping plover nesting habitat. We found that modest SLR (3.0–4.1 mm/ yr based on present rates) may increase suitable piping plover nesting habitat area in 50–100 years and that some beach management strategies influence habitat availability.

Introduction

Barrier islands span 3700 km and cover 6800 km² along the U.S. Atlantic and Gulf Coasts (Zhang and Leatherman 2011). These islands, with their associated bayside marshes and tidal flats, provide many services for humans and wildlife, including nutrient retention and cycling, recreational activities, and habitat for imperiled and commercially valuable wildlife (Hassan et al. 2005, White et al. 2010, Barbier 2012). Many rare species in the U.S., 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 barrier islands (USFWS 1996).

Approximately 22.4 million people live in areas bordering the open ocean or directly subjected to coastal flood hazards (Crowell et al. 2010) and approximately 1.4 million people live on barrier islands along the U.S. Atlantic and Gulf Coasts. Human populations have been increasing steadily in 16 of the 18 coastal states (i.e., all U.S. Atlantic and Gulf coast states except MS, RI) where barrier islands are abundant (Zhang and Leatherman 2011). Barrier islands are frequently modified to support infrastructure development for these growing populations (e.g., Slott et al. 2010). Maintaining these modifications 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 (Godfrey 1976, Davis 1994, FitzGerald et al. 2008). The position of these islands between the open ocean and the mainland, and their generally low elevation, make them morphologically responsive to storms (Morton and Sallenger

2003, Stockdon et al. 2009, Doran et al. 2012) and sea-level rise (CCSP 2009, Williams 2013). This barrier island sensitivity to SLR, along with the millions dollars spent annually to maintain wildlife habitat and recreational areas, have potentially significant consequences for humans and wildlife, and for piping plovers in particular (Titus et al. 1991, Hecht and Melvin 2009, Gieder et al. 2014, Schupp et al. 2013).

Mean global sea level for the years 2046–2065 is projected to be 0.24–0.29 m higher than it was from 1986–2006, with a predicted increase to 0.43–0.73 m by 2100 (IPCC 2013). The relative SLR rate at a given location is influenced by regional variations stemming from broader ocean circulation patterns, inter-annual variability (Zhang and Church 2012, Ganachaud et al. 2013), glacial isostatic adjustment, tectonic movements, and by local variations stemming from land subsidence, geologic setting, sediment supply, and subsurface resource extraction (IPCC 2013). Sea level changes affect areas by inundation, or driving morphological changes that reshape the coastal landscape. These processes may cause beach erosion and land loss, altering the morphology of low-lying habitats (CCSP 2009, IPCC 2013, Melillo et al. 2014). Barrier islands along the U.S. Mid-Atlantic Coast with small tidal ranges, large waves, low elevation and slope, and historically high SLR rates are particularly vulnerable (Thieler and Hammar-Klose 1999; Gutierrez et al., 2011). Accurately forecasting how SLR will alter barrier islands over the 21st century is difficult due to morphological differences from one island to the next and the broad range of physical and ecological processes that produce varying effects across islands (Nicholls 2010, Stutz and Pilkey 2011).

While the effects of SLR alone on barrier islands will be significant, on yearly to decadal time scales storms and beach stabilization efforts in response to storms also influence barrier island morphology (Slott et al., 2010; Doran et al. 2012). A major concern for coastal regions will be the interaction between SLR and storms of varying frequency and intensity (IPCC 2013). Extreme water levels in areas with relatively high SLR rapidly alter barrier islands by opening inlets, restructuring dune habitats, and inundating areas (FitzGerald et al. 2008, Colberg and McInnes 2012). Although these are natural processes, accurately predicting these changes remains challenging. Furthermore, storm patterns are generally unpredictable, making reliable predictions related to storm/SLR interactions especially difficult (IPCC 2013). A majority of barrier islands along the U.S. Atlantic Coast have been altered by beach stabilization strategies (e.g., sea walls, groins, and beach nourishment; USFWS 2012). Beach nourishment actions range from off-shore, near-shore, and on-shore sand deposition to construction of artificial sand dunes (Nordstrom 2000, Psuty and Ofiara 2002). Understanding how beach stabilization alters barrier island response to SLR and storms is an inherent component in forecasting change (Plant et al. 2014, McNamara et al. 2011, Slott et al. 2008, 2010, Magliocca et al. 2011).

We combined our understanding of SLR, storm, and barrier island stabilization impacts to develop the capability to forecast endangered species habitat suitability. The piping plover (hereafter "plover") was listed in 1986 as threatened along the U.S. Atlantic Coast under the U.S. Endangered Species Act (USFWS 1985), and was chosen as the focal species for this study because they nest in sparsely vegetated, low elevation areas on barrier islands, and have been a persistent focus of coastal habitat management efforts (Wilcox 1959, Kumer 2004, Houghton 2005, Cohen et al. 2009, Schupp et al. 2013). Previous studies investigating SLR effects on wildlife species did not explicitly link what was known about plover habitat preferences to SLR and storm driven changes in barrier island morphology. Instead, these efforts assumed an average historic SLR rate, static geomorphology, or modeled dynamic response using simplified beach or barrier island geometries (Seavey et al. 2011, Benscoter et al. 2013, Reece et al.

2013a,b, Sims et al. 2013, Gieder et al. 2014). Though these studies furthered our understanding of how SLR may affect barrier island wildlife habitat, we developed a modelling framework to improve the ability to predict specific barrier island geometries under future SLR, storm, and management scenarios and to evaluate future plover habitat suitability.

We developed three linked models, using Bayesian Networks (BNs) to integrate processes on different spatial and temporal scales, and forecast changes to barrier island morphology in response to SLR and erosion management efforts. BNs are an ideal modeling framework for achieving these goals because they allow combinations of continuous and categorical classifications and they incorporate the uncertainty inherent to predicting dynamic changes (Pearl 1988, Uusitalo 2007, Koller and Friedman 2009). Our first BN, hereafter the "shoreline change BN," calculates the probability of a specific shoreline change rate based on knowledge of historical sea-level rise rates and coastal geometry and hydrodynamic conditions sampled at a coarse spatial scale (i.e., 5-km; Gutierrez et al. 2011). Our second BN, hereafter the "geomorphology BN," uses the shoreline change probability distribution (output from the first model) in combination with 11 barrier island geomorphological metrics (e.g., physical characteristics such as beach width, elevation, etc.) and knowledge of beach management history (i.e., beach nourishment or foredune construction) to predict probabilities of morphological characteristics at a finer resolution (i.e., 5-m^2; Gutierrez et al. In Review). Our third BN, hereafter the "plover BN," used the geomorphology BN probabilities to predict subsequent changes to wildlife habitat, particularly piping plover nest site suitability (Gieder et al. 2014).

Our linked BNs incorporated dynamic responses by feeding changes through a network of linked variables at multiple scales. Each of the three BNs was developed and individually tested prior to this study to determine their suitability for modeling dynamic SLR driven change and plover response to that change (Gutierrez et al. 2011, Gutierrez et al. in review, Gieder et al. 2014). Our first objective was to link the three BNs and evaluate them by first hindcasting and verifying the probability of suitable nesting habitat on a portion of Assateague Island where the plover BN (Gieder et al. 2014) was originally developed and then extend this evaluation across the whole island. Our second objectives was to evaluate the sensitivity of the linked BNs by testing individual variables for accuracy and comparing error rates at different stages of the linking process. Finally, our third objective was to use this linked BN to forecast various SLR rates and beach nourishment effects on plover nesting habitat in the next 50–100 years.

Methods

Study Area

We used data from 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 Virginia, and the National Park Service (NPS) manages Assateague Island National Seashore (ASIS) on most of the Maryland portion, except for a small portion managed by the state of Maryland as Assateague State Park. Assateague Island's habitats include bayside tidal marsh and mudflats, interior coniferous and deciduous forest, and ocean-fronting dunes and sandy beaches (Morton et al. 2007). The island has relatively 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. Assateague Island has required sustained efforts to maintain the barrier over the last 80+ years in response to storm driven modifications to the island (e.g., overwash and breaching; Dean and Perlin 1977, Krantz et al. 2009, Schupp et al. 2013). These modifications have affected barrier morphology on portions of the north end of the island.

Bayesian Network Models

We used Netica 4.16 to construct separate BNs that calculated probabilities of barrier island 1) shoreline change (Gutierrez et al., 2011), 2) geomorphological characteristics (Gutierrez et al., in review) and 3) plover nesting suitability (Gieder et al., 2014; Figure 2). Using code in MATLAB 8.2, we linked these BNs such that sea-level rise influences shoreline change probabilities, shoreline change (and other factors, see Gutierrez et al., 2011) influences predictions of geomorphology, and geomorphology (and other factors) influences the plover BN, with a final outcome being predicted probabilities of suitable and unsuitable plover nesting habitat. Each of the linked BNs is described here.

Shoreline change BN

The shoreline change BN consisted of 5 variables (Figure 2, Table 1) that estimate future shoreline change probabilities based on historical observations from the U.S. Atlantic coast. Shoreline change rate is the rate of change in shoreline position (m/yr) since 1850 and was based on historical shoreline data used in previous coastal vulnerability studies (Thieler and Hammar-Klose, 1999). The shoreline change BN, developed by Gutierrez et al. (2011), incorporated relative SLR rate (m/yr), wave height (m),tide range (m), geomorphic descriptions (e.g., rocky cliffed coasts, cobble estuarine beaches, sandy barrier island beaches), and coastal slope (%). This network was constructed using data sampled and averaged over 1–5-km coastal segments from Maine to Florida from the 1850s–1980s, with exact dates varying by specific locations (see references in Gutierrez et al. 2011). The outputs of this model was probability distributions for various shoreline change rates every 5 km along the U.S. Atlantic Coast (Gutierrez et al. 2011).

Geomorphology BN

The geomorphology BN used information from remote sensing datasets to describe the physical characteristics of Assateague Island. This BN was modified from a BN developed by Gutierrez et al. (In review) and used the shoreline change rate (m/yr), an output from the shoreline change BN, beach height (m), dune crest height (m), island width (m), type of anthropogenic modification (hard infrastructure or engineering efforts), and distance to inlet (m) to calculate the probability distributions of outputs including beach width (m), elevation (m), beach slope (%), distance to ocean shoreline (at mean high water line, m), habitat type (wetland, shrub/forest, sandy barrier) and vegetation type (sparse, herbaceous, shrub/forest, shell bed) (m; Figure 2, Table 2). The latter four variables were added to this BN for this study because they were required by the plover BN (Figure 2, Table 2). Data for this BN were sampled along cross-island transects spaced 50 m apart for the entire length of the island (Gutierrez et al., In review). Variables that were defined locally (elevation, beach slope, vegetation type, and habitat type) were calculated at the scale of 5x5-m cells along each transect and were associated with the remaining variables defined only at the transect-scale. A combination of lidar, aerial photo, and survey data from 1999, 2002, and 2008 were sampled to construct the datasets that were used to train (i.e., where the model establishes probabilistic relationships between variables based on a dataset) and then implement the BN.

Plover BN

The plover BN was constructed using nesting data provided by NPS staff, lidar, and aerial photography datasets at ASIS from 1999, 2002, and 2008 on the northern 10 km of the island, hereafter “the North end,” and illustrates how nesting habitat relates to physical variables (Table 3, Figure 2; Gieder et al. 2014). We used data from the North end because it is an established plover nesting area, and data for this area were more complete than the rest of the island.

Each physical variable was derived at either the 50-m transect (see geomorphology BN description) or 5x5 m scale. These variables were then associated with nest locations in 1999, 2002, and 2008 as well as an equal number of random points without nests that were generated for each year. We limited random points to open and vegetated areas of the North End, but excluded freshwater ponds and forests, since these are areas where plovers would never nest. The transect-scale variables in the original model (Gieder et al. 2014) included beach width (m), distance to the dune crest (m) and to the dune toe line (m), distance (m) to the bay and the ocean shoreline (at the mean high water line, m), distance to the mean low water bay shoreline (m), and distance to moist substrate habitat (m). The 5x5 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 3). We defined site fidelity by 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).

In order to link the plover BN in this study to the geomorphology BN, we modified the ‘simple model’ described above and in Gieder et al. (2014) by adding a habitat type variable (wetland, shrub/forest, sandy barrier), to account for the lack of detailed vegetation data across the entire island. We also altered the bin ranges of certain variables in the geomorphology and plover BN from ranges presented in Gutierrez et al. (in review) and Gieder et al. (2014) to match the inputs and outputs for the linked models (Table 1–3). For example, the elevation ranges in the geomorphology BN (-2.5–29 m) and the plover BN (-0.5–5.8 m) were initially different, so we increased the elevation range in the plover BN to match that of the geomorphology model which sampled the entire island, not just the North end where the plover model was originally developed. We present the actual data ranges for North end plover nest and random sites in Table 4 for comparison to other nesting areas where these models may be applied. The final plover model in this paper includes beach width (m), distance to the ocean shoreline (m), elevation (m), habitat and vegetation type, and slope (%; Figure 2; Appendix I). These variables were chosen because previous studies have found them to be important determinants of nesting habitat quality (Patterson et al. 1991, Cohen et al. 2009, Maslo et al. 2011) and they were also shown to be the most influential variables in this model (Gieder et al. 2014). We excluded one key determinant of nesting habitat quality, moist substrate (MOSH), found by many previous studies (Patterson et al. 1991, Loegering and Fraser 1995, Keane 2002, Cohen 2005, Fraser et al. 2005, Cohen et al. 2009). Cohen et al. (2009) used aerial photographs to delineate MOSH but we could not clearly delineate MOSH on the North End of Assateague using this method, so we used the spectral reflection of color infrared photographs instead. We used a supervised classification method to extract all wet substrate over the entire North End, including inland and intertidal areas. We excluded MOSH from our model because we could only extract it for 2008 and because model error only increased to 4% (from an original error of 3%) when MOSH was excluded (Chapter 2, Gieder et al. 2014). There was a correlation between MOSH and distance to the mean high (Pearson correlation coefficient; $r = 0.66$, $n = 140$, $p < 0.001$) and mean low water (Pearson correlation coefficient; $r = 0.68$, $n = 140$, $p < 0.001$) tideline on the bayside were correlated with distance to MOSH in Gieder et al. (2014) so we considered these variables to serve as a proxy for MOSH.

Linking BN Models

The 3 independent models make predictions in the form

$$P_m(Y_i|X) = \frac{P_m([X_{1,j=1,}X_{1,j=2,} \ldots X_{2,j=1,}X_{2,j=2,}\ \ etc.]|Y_i)\ P_m(Y_i)}{P_m(X)}$$

where Y_i is a model outcome (e.g., Y = "nest attempt", 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). 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 can take on a finite number of states denoted by index j. The right side [Eq. 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 denominator is the probability of finding a particular set of inputs. The algorithm used in Netica factors the terms on the right of equation 1 based on the connections between nodes (Charniak 1991). Hence, it is possible to take a probability, for example $P_{m-1}(X_{1,j}|W)$, and feed this value into the right side of equation 1 anywhere that $P_m(X)$ is required, where W denotes the inputs to model m-1.

The shoreline change model was linked to the geomorphology model using the shoreline change rate variable present in both models. We then used the following common variables to link the geomorphology model to the plover model: beach width (m), distance to ocean (at mean high water line, m), elevation (m), beach slope (%), vegetation type, and habitat type (Figure 2 and Table 1–3). Because the models were linked, the uncertainty from one model was passed to the next model in the form of probability density functions. Part of our analysis probed the sensitivity of the final prediction (probability of suitable and unsuitable nesting habitat) to the uncertainty propagated through the linked BNs by evaluating the hindcast error of the geomorphology and plover BNs alone and then comparing that error to that of the linked BNs. The error rate for the geomorphology BN was calculated as the percent of cases where the most likely predicted outcome (i.e., the bin with the greatest posterior probability) did not match the observed bin value in the dataset, whereas error rates for the plover BN were computed as the number of predicted unsuitable and suitable habitat predictions that did not match the nests and random points without nests in the dataset.

Hindcasting scenarios

We hindcasted by training the linked BNs using nesting data from all 3 years (1999, 2002, 2008) and then predicted habitat suitability probabilities for each year based on input from each year's observed geomorphology, and finally compared against actual nests for that year, as per Gieder et al. (2014). We hindcasted on the North end where the original plover model was developed and then extended our hindcasting over the entire island, with 3 focus areas outside of the North end examined for congruence with actual nesting suitability as described below. We assessed the linked BN performance on the North end by computing plover nesting habitat suitability prediction error rates as in Gieder et al. (2014) for a) the plover BN informed with geomorphology data, b) the linked geomorphology and plover BN, and c) three linked BNs. These error rates were generated from the actual nest and random points by quantifying the proportion of false positives (where the BN predicted suitable habitat when there was no actual nest presence observed), false negatives (where the BN predicted unsuitable habitat when there was a nest observed), true positives, and true negatives (predictions that match the actual data). We additionally tested the error of individual variables in the geomorphology BN to assess whether any might be contributing disproportionately large error to the plover predictions. This error was computed by quantifying the percentage of predictions that fell outside of the observed input bin values.

When hindcasting across Assateague Island, we focused our analyses of prediction accuracy at two established nesting sites on CNWR: 1) a narrow strip known as “the overwash” and 2) the southern portion of the island known as “the hook” (Figure 1) located on the southern end of Assateague Island. The overwash is a narrow (approximately 150 m) strip of land with open beach on the ocean-side, low dunes in the center, and sparsely vegetated intertidal to supratidal flats on the bayside. The hook is immediately south of the overwash and is wider (approximately 1300 m) than the overwash, with a larger complex of dunes, wider open beach on the ocean side, and a comparatively more varied array of habitats. We also hindcasted at a third sporadically occupied nesting area in a 19-km portion of ASIS known as “the over-sand vehicle (OSV) zone”. The OSV-zone is wider and supports more diverse habitats than the North end, and plovers only nested in small numbers (1–5 nests) before 2012. Our intent was to predict a range of suitable nesting habitat and evaluate those predictions using actual nests in these different nesting sites.

The hindcasting and forecasting results are presented by dividing the island into sections spanning 1 km of ocean shoreline. Within each section, we extracted results from all predicted points and calculated the percentage of all points where the predicted probability (p) of suitable habitat exceeded 0.5. In other words, we identify the percentage of potentially suitable nesting habitat within each 1 km section of island. We used the same sections in each hindcast year and color-coded the resulting 53 island sections according to the range of suitable habitat percentage within each, from 0–10, 10–20..., and 90–100% (Figure 3). Thus, if 65% of all points in a section had a p (nesting habitat suitability) > 0.5, then it was color-coded as the 60–70% range. We used this same procedure for other variables in the model that may influence suitable habitat probability, such as vegetation type to determine what factors might be driving changes in habitat suitability.

Forecasting scenarios: North end

We first predicted shoreline change probabilities in the shoreline change model under relative SLR rates of (1) 3.0 mm/year, the average relative SLR along U.S. East coast islands over the past 151 years (Zervas 2009, NOAA 2014) and (2) 4.1 mm/year, an approximately 25% higher-than-present coast-wide SLR rate. We then input the shoreline change rate probabilities into the geomorphology BN and passed the resulting output into the plover BN to obtain habitat suitability probabilities.

Beach nourishment strategies employed at Assateague Island (and elsewhere along the U.S. Atlantic and Gulf Coasts) include, for example, near-shore sand deposition and foredune construction. At Assateague Island, this has occurred on the North end (Schupp et al. 2013) to replace sediment lost to a jetty that maintains Ocean City Inlet on the northern tip of the island (-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). After major storm events in January and February 1998, the U.S. Army Corps of Engineers constructed a foredune at a height of 2.05 m over the 2.4 km section of the North end that was most susceptible to overwash and implemented a long-term plan to address the sediment starvation cause by the inlet (Schupp et al. 2013).

We used 2 erosion management strategies, specified through inputs to the geomorphology BN's dune crest height, elevation, and anthropogenic modification variables (Figure 2, Table 2) based on these activities: 1) biannual near-shore sand deposition (60,000 m^3/event, hereafter "SD") along the entire North end and 2) increasing the foredune height to 4 m with 6 notches cut into the dune to an elevation of 2.5 m (FD, notched areas comprise approximately 30% of the total foredune length). To specify the notches in our BN inputs, we altered the elevation of the regions of the barrier that coincided with the foredune location and notch locations coinciding with a 2005 notch elevation survey (NPS 2005). Since our input data were sampled at 50 m intervals along shore, we specified the notches at locations where a 50 m spaced transect intersected a notch location. However, we varied the height and depth of the actual notches, and assumed that they were self-maintaining, or would be maintained, and would not change in area or shape over time (Schupp et al. 2013).

We compared the forecasted plover nesting habitat suitability probabilities for all combinations of the 2 SLR rates and 2 beach nourishment strategies across the North end using island section maps as described above. The same transects points were used for these forecasts as were used for 1999, 2002, and 2008 so the shape of the island in the output maps did not change. We report the sections on the North end that fell within each percentage range under 6 future scenarios (i.e., 2 SLR rates x 3 beach nourishment strategies (no management, SD, FD) and then compared these results to those for 2008, 2002, and 1999.

Results

We simulated six linked hindcast scenarios (3 years, 2 regions) and six forecast scenarios (no management, sand deposition (SD), foredune (FD) × 2 SLR rates) for 1999, 2002, and 2008. The resulting nesting habitat suitability probabilities were derived from unique conditions within the shoreline change (18,770), geomorphology (5,508,055), and plover (1,506,948) BN's, respectively.

Hindcast Error Evaluation: Geomorphology BN Alone

Overall error rates (i.e., where predictions fell outside of the observed input bin values) for dune crest height (m), beach width (m), and beach height (m) for 1999, 2002, and 2008 were comparable to those reported by Gutierrez et al. (In review) and were relatively consistent from dataset to dataset varying 2–4% (Table 5). Elevation (m) error rates ranged from 28–40% with the lowest rates for the 2008 dataset. Error rates for beach slope (%) were consistently the highest ranging from 46–52%. Error rates for vegetation type spanned the widest range from 25% for 1999 to 50% for 2008. Habitat type error rates were consistently the lowest ranging from 27–28.5% (Table 5). Specific error rates computed using only nests and random points yielded similar results with the exception that vegetation had higher error in 1999 (74–78) compared to 2002 and 2008 (42–48) and beach slope had higher variation among years, 26–31 in 1999, 49–50 in 2002, and 54–57 in 2008 (Appendix 3). These error rates were similar for the geomorphology BN alone and the linked BNs (Appendix 3 and 4).

Hindcasting: All areas

North end plover habitat suitability probabilities were tested against data sets from each year that included 72, 61, and 70 nests and equal number of random points without nests in 1999, 2002, and 2008, respectively. Error rates for the plover BN alone were lowest, with a range from 14.3% when predicting habitat suitability in 2008 to 21.4% in 2002 (Table 6). These error rates were higher for the linked geomorphology and plover BN, ranging from 34.0% when predicting habitat suitability in 2008 to 44.3% in 2002. Error rates for the three linked BNs, the shoreline change BN, the geomorphology BN, and the plover BN were similar to the linked geomorphology and plover BN. For all error rates, false positives (i.e., predicted suitable habitat when a nest was not present) dominated the total error. False negatives (i.e., predicted unsuitable habitat when a nest is present) remained low for all years and models, with a maximum of only 12.3% in 2002 for the three linked BNs (Table 6). Predicted suitable habitat (sample points with p (suitable habitat) > 0.5) within each of the total 10 sections on the North end declined from 1999 to 2008. In 1999, 2 sections had mostly suitable nesting habitat (> 60% of points), whereas, by 2008, all sections had less than 40% suitable points (Figure 4, Table 7).

Across the island, all of the actual plover nests in our focal nesting areas fell in sections predicted to have a majority of suitable habitat (> 50% of points with p (suitable habitat > 0.5, Table 7, Figure 5a-c, Appendix 2). Few nests were observed in island sections predicted to have low suitability (< 10% of points with p (suitable habitat > 0.5)). In 2008, an area on CNWR known as Wild Beach and a nearby artificial nesting area had 7 nests despite having < 10% predicted suitable points in the section (Table 7). Also, a section in the ASIS-OSV zone that was predicted to have fairly low suitability in 2008 (< 20% suitable points) held no actual nests that year, but plovers did nest in this area in 2012 and 2013 (Figure 6).

Forecasting: linked shoreline change, geomorphology and plover models

With 3 mm/year and 4.1 mm/year SLR, suitable nesting habitat was predicted to increase in all sections on the North end compared to 1999, 2002, and 2008. In all forecasted scenarios, 7 of the 10 sections on the North end were mostly suitable habitat (> 50% points with p (suitable habitat) > 0.5) compared to 3 sections for hindcasts in 1999, 1 in 2002, and none in 2008. Forecasted percentages of suitable habitat with 3 mm/year and 4.1 mm/year SLR, and both SLR rates and the FD (foredune) scenario were very similar (FD; Table 8). Only the scenario with SD (sand deposition) differed in that the sections with the most suitable habitat had no more than

70% suitable nest points compared to 80% suitable nest points for the other scenarios. The mean and variance (±SD) of all predicted point probability values were also similar (ranging from 0.58±0.07 to 0.65±0.09) in all scenarios and in all 10 island sections (Table 9). In all scenarios, there were substantially higher percentages of suitable habitat forecasted on the North end compared to predicted suitability for 1999, 2002 and 2008 (compare Figure 7 to Figure 4, Table 8).

Compared to 2008 (the most recent year in our dataset), there is much less herbaceous vegetation in all forecast scenarios (Figure 7). All sections in 2008 had at least twice as many sample points that were herbaceous compared to forecast scenarios. Six of the ten sections predicted more herbaceous vegetation with 3mm/yr SLR and SD than with 3 mm/yr alone, whereas all of the sections had more herbaceous vegetation in 2008 compared to that predicted for all forecast scenarios. All of the sections also had less sparse vegetation and more woody vegetation in 2008 compared to the forecast scenarios, except for one section that had more woody vegetation with 3 mm/yr SLR and SD. Sections that differed between 3 mm/SLR alone and 3/mm SLR with SD had more points that were predicted to be herbaceous and woody vegetation under the SD scenario compared to SLR alone (Table 7). There was no difference with 4.1 mm SLR/yr and frequent sand deposition, or in predicted vegetation under this scenario (Table 10).

Discussion

Overall, our linked BNs hindcasted high probabilities of suitable nesting habitat for a majority of known nesting areas across Assateague Island, and low suitability for those areas where plovers were absent. When tested specifically against actual nest data on the North End, the plover BN informed with geomorphology data produced predictions with low error rates.

The increased error when predictions were made with the linked BNs illustrated that uncertainty increases as the scale is enlarged from specific nest sites. This information loss is to be expected and reflects inherent uncertainty when predicting change in complex systems. Error rates for the linked BN's were low for predicting suitable habitat. Accurately predicting suitable habitat is a vital aspect in considering future piping plover nesting habitat management.

Our hindcasting accurately predicted higher percentages of suitable nesting habitat in sections where plovers nested and also in more recent nesting areas that became occupied following habitat changes on the North end that reduced nesting habitat quality (Gieder et al. 2014). Relatively high reproductive output (fledglings/pair) from 2009–2011 on both ASIS and CNWR may have driven plover expansion into these areas. Reproductive output increased from 0.4–1.3 fledglings/pair on ASIS between 2008 and 2011 and from 0.59–1.73 fledglings/pair on CNWR between 2008 and 2010 (K. Holcomb, CNWR, unpublished data and J. Kumer and T. Pearl, ASIS, unpublished data). Fledged chicks returning to their natal sites following high productivity years could have expanded into the previously unused suitable habitat in the ASIS OSV zone, as breeding plovers in Saskatchewan, Canada, have been shown to expand into new areas following highly productive years (Cohen and Gratto-Trevor 2011).

Our aim with this study was to develop and analyze broad scale (i.e., 1 km island sections) forecasts of plover nesting habitat at a specific location (the North End) on ASIS. The high error rates for specific variables such as beach slope and the high variability in error for vegetation type indicate that the current data probably do not capture the full geomorphic variability on the North End. Furthermore, more points were predicted to have a suitable habitat probability of 0.5 in hindcasting across the rest of Assateague Island, indicating that there was not enough data at these locations to yield a probability in favor of suitable or unsuitable nesting habitat. Finally, the plover BN incorporated several assumptions about plover nesting biology that may need to be addressed if nest predictions are desired at a more detailed scale. For example, we assumed that there was no minimum patch size for nesting territories. Plovers require a minimum nesting patch size and will not nest in small open patches surrounded by dense vegetation (Cohen et al. 2009). Incorporating territory size may improve the accuracy of suitable habitat predictions at a smaller scale by allowing us to evaluate the spatial availability of suitable nesting patches. This may allow us to incorporate time lags in plover response to shifting habitat suitability in other areas, as our results showed that high site fidelity to the northern portion of ASIS may have been the reason why suitable nesting habitat in 2008 in the OSV zone did not support nesting plovers until 2012 and 2013.

The increase in suitable plover habitat we found under modest future SLR rates is similar to Seavey et al. (2011). Our study of Assateague Island differed from Seavey et al. (2011, conducted at Long Island, NY) as we addressed the lower end of this SLR range (0.3 – 0.41 m) and added dynamic response via shoreline change linked to geomorphological evolution of the barrier island, and local nest site selection. Seavey et al. (2011) relied on a more simplified approach making assumptions that habitat would either be submerged or would shift upwards and landward yet maintaining the same geometry. In contrast, our approach included forecasts of barrier island geometry to model a complex habitat response. For example, we show the mechanism underlying predicted suitable plover habitat increases is related to vegetation changes under modest SLR rates compared to those SLR rates with biannual, near-shore sand deposition (Figure 7d). A combination of other variables are likely related to habitat increases, particularly for years when vegetation had higher error rates.

The increases in suitable nesting habitat that we forecasted for plovers in 50–100 years does not necessarily translate into a productive population of plovers in the interim or the future (Rodenhouse 2000). Firstly, the increases in suitable habitat we forecasted include variably suitable habitat. The mean probability of suitable habitat for each island section under each scenario was fairly low, indicating that there will be little highly suitable habitat. Secondly, we cannot know whether the biannual near-shore sand deposition or heavily-notched foredune will initially result in declining habitat quality, as observed from 1999–2008. Our results show only how those management scenarios combined with 3–4.1 mm/yr SLR over 50–100 years, and including the uncertainties incorporated with the BN models, will likely shape habitat in 2049–2108. Short-term, interim habitat predictions would be highly variable and inaccurate under our current modeling framework, because variables in the model such as sea-level rise produced measurable change over long periods. The variation in these variables over shorter periods contributes a lot of uncertainty to predictions. However, BN's could be well suited to developing short-term, interim habitat predictions as more information is gathered. With further understanding of how barrier island geomorphology responds to SLR over decadal time scales, the model we present could form the basis for future models that inform our understanding of how habitat responds over shorter time frames.

The SLR rates used in our forecast (0.3–0.4 m) are lower than recent projections ranging from 0.43–0.73 m higher than present by 2100 (NCA 2012, Horton et al. 2013, IPCC 2013, Jevrejeva et al. 2014). Because the BNs in this study were based on field data, we are currently unable to make reliable predictions of higher SLR rate effects on shoreline change, geomorphic response, or plover habitat suitability along the U.S. Atlantic Coast. Updating our BNs with data from areas with higher rates of SLR and observed coastal response, for example the U.S. Gulf

Coast, could improve the quality of predictions under such higher rates (Lorenzo-Trueba and Ashton 2014).

Implications for habitat and species management

Our results relating near-shore sand deposition to decreased plover nesting habitat availability coincide with other studies demonstrating nesting habitat decreases following beach nourishment (Cohen et al. 2009; Schupp et al. 2013). Our findings of decreased suitable nesting habitat on the North end from 1999–2008 after the construction of an un-notched artificial foredune and biannual nearshore sand deposition indicate potential negative effects of certain types of beach management strategies. However, there are a wide range of other beach management strategies that could have different effects on nesting habitat suitability. For example, maintaining open inlets, modifying dune/beach elevation and structure to encourage more frequent overwash, and controlling vegetation growth are just some beach management strategies that may result in more open sparsely vegetated low elevation habitat that nesting piping plovers prefer (Houghton et al. 2005, Cohen et al. 2009, Schupp et al. 2013).

Our findings provide a starting point for predicting how plover nesting habitat will change in a context of planned human modifications intended to address climate change-related threats (USFWS 2009). We have not considered all possible forms of habitat management nor all possible SLR scenarios, so these results should not be used to make inferences about current or planned beach management activities. But, our approach takes a vital step in that direction by outlining a model by which these inferences can be made. Further analyses under varying beach management scenarios could show the implications for nesting plovers, thus informing managers considering various storm protection scenarios for this species and others that are dependent on coastal morphology and vegetation interactions. Our demonstration of fine- to coarse-scale, site-specific future predictions of island geomorphology and plover habitat suitability using relative SLR will be useful to managers coast-wide, and these linked models are being tested and expanded to other plover nesting locations, including sites from Massachusetts to North Carolina.

Conclusion

We have developed three linked Bayesian Networks (BNs) that predict and link SLR impacts and storm effects on (1) shoreline change to (2) changes in barrier island geomorphology, including the effects of erosion management efforts, and finally to (3) changes in piping plover habitat suitability. This model is the first that we know of to incorporate sensitivities to dynamic barrier island response in forecasting changes in avian response. Our model accurately predicted higher percentages of suitable nesting habitat in sections where plovers nested and also in more recent nesting areas that became occupied later. Our model was able to predict suitable habitat with low error rates, and most overall prediction error was associated with false positive predictions, or predicting a nest was present when no nest was present. Additional data for specific geomorphic variables that had high uncertainty (e.g., a more varied array of slope) could lower the false positive error. Our forecasting showed that modest SLR rates may increase suitable piping plover nesting habitat area on ASIS in 50–100 years and that some beach management strategies may influence habitat availability. Further model developments will focus on forecasting additional SLR rates and management strategies to broaden the applications of this model to other barrier islands along the U.S. Atlantic Coast.

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Tables

Table 1. 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*) nesting habitat suitability.

Variable	Bin categories				
	1	2	3	4	5
Relative sea-level rise rate (mm/yr)	0–1.80	1.80–2.50	2.50–2.95	2.95–3.16	3.16–4.10
Coastal slope (%)	0–0.025	0.025–0.040	0.040–0.070	0.070–0.200	0.200–0.411
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	1.25–1.60
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 of erosion, rocky, cliffed coasts, fjords; Geo 2, low risk of erosion, medium cliffs, indented coasts; Geo 3, moderate risk of erosion, low cliffs, glacial drift, alluvial plains; Geo 4, high risk of erosion, cobble beaches, estuarine and lagoonal coasts; Geo 5, very high risk of erosion, barrier beaches, sand beaches, salt marsh, mud flats, deltas, mangroves, coral reefs (Gutierrez et al. 2011).

Table 2. 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*) nesting habitat suitability. We parameterized the network using a 3-year dataset from 1999, 2002, and 2008 on Assateague Island National Seashore, MD (Gutierrez et al. In Review).

Variable[a]	Bin categories						
	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 modification	Construction + occasional modification	Frequent modification	Construction + frequent modification	n/a
Elevation (m)	-2.5–(-0.5)	-0.5–0.5	0.5–1.5	1.5–2.5	2.5–3.5	3.5–29.0	n/a
Beach width (m)	0–50	50–100	100–150	150–200	200–600	n/a	n/a

Beach slope (%)	0–2.5	2.5–5.0	5.0–7.5	7.5–20.0	20.0–90.0	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

[a] “Shoreline change rate (m/yr)” is the rate of change in shoreline position (m/yr) since 1850 and is based on historical shoreline data used in previous coastal vulnerability studies (Thieler and Hammar-Klose, 1999), “Island width (m)” is the straight line distance from the ocean mean high water (0.34 m referenced to NAVD88; [Weber et al. 2005]) line to the mean high water line on the bayside along each cross-island transect, “Beach height (m)” is the elevation midway between mean high water (0.34 m NAVD88; [Weber et al. 2005]) and the dune toe elevation. “Distance to inlet (m)” is the along-shoreline distance of each mean high water shoreline position on each transect to an artificial inlet on the northern tip of Assateague Island, “Dune crest height (m)” is the high elevation point at the top of the dune, [Stockdon et al., 2009; Stockdon et al., 2007]), “Anthropogenic modification” reflects the presence of hard infrastructure (construction), such as paved roads and buildings, as well as constructed berms or dunes, and shoreline engineering efforts (modification) occurring over the last 30-40 years, “Elevation (m)” is the vertical height above sea-level; “Beach width (m)” is the horizontal distance between the dune-toe boundary and the mean low water line, “Beach slope (%)” is the average rise over run between consecutive points along each transect, “Distance to mean high water ocean (m)” is the perpendicular distance from the mean high water ocean boundary.

Table 3. Variables and bin categories for the piping plover Bayesian Network included in our linked model used to predict the effect of changing barrier island geomorphological variables on piping plover (*Charadrius melodus*) nesting habitat suitability. We parameterized the network using datasets from 1999, 2002, and 2008 containing observed nest locations and random points that did not contain nests on Assateague Island National Seashore, MD.

Variable[a]	Number of observed values (n)			Bin categories[b]						
	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 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	3.5–29.0	n/a
Nest attempt	144	122	140	Absent	Present	n/a	n/a	n/a	n/a	n/a
Beach 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 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); "Slope (%)" is the average rise over run within a 5 m radius 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] Bin categories are non-overlapping.

Table 4. Average and range for the continuous variables extracted from field- and remotely-sensed data on the North end of Assateague Island National Seashore, at piping plover (*Charadrius melodus*) nest sites, and sites without nests, that were used to inform the plover BN.

Variable[a]	1999[b]		2002		2008	
	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
Beach 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; “Beach slope (%)” is the average rise over run within a 5 m radius of a nest or random point without nest.

[b] Year of model prediction

Table 5. Error rates (percentage of predictions that fell outside the observed input bin values, %) for individual variables in a geomorphology Bayesian network based on three years of data from Assateague Island National Seashore, MD, USA.

Variable[a]	1999[b]	2002	2008
Dune crest height (m)	34.4	32.4	34.5
Beach width (m)	23.6	25.8	26
Beach height (m)	35.2	33.2	36.4
Elevation (m)	39.7	36	28.2
Beach slope (%)	46.7	50.1	52.4
Vegetation type	24.9	37.3	49.5
Habitat type	28.1	28.5	27.2

[a] "Dune crest height (m)" is the elevation of the foredune crest (Stockdon et al., 2007) "Beach width (m)" is the horizontal distance between the dune-toe boundary and the mean low water (MLW) line; "Beach height (m)" is the mean of the dune toe and MHW line elevations; "Elevation (m)" is the vertical height above sea-level of a nest or random point without nest; "Beach slope (%)" is the average rise over run within a 5 m radius of a nest or random point without nest; "Vegetation type" is the general type and density of vegetation at a nest or random point without nest; "Habitat type" is the general habitat type at the nest or random point without nest.

[b] Year of model prediction.

Table 6. Error (percentage of predictions that fell outside the observed input bin values, %) associated with predictions of piping plover (*Charadrius melodus*) nesting habitat suitability. Predictions were generated from A) the piping plover BN informed with geomorphology data, B) the linked geomorphology and piping plover BN, and C) three linked BNs, the shoreline change BN, the geomorphology BN, and the piping plover BN for the North end of Assateague Island National Seashore, MD in 1999, 2002, and 2008.

Year[a]	. A. PIPL BN Error[b]			B. Linked BN (GEO=>PIPL) Error			C. Linked BN (SLC=>GEO=>PIPL) Error		
	Total	False positives	False negatives	Total	False positives	False negatives	Total	False Positives	False negatives
2008	14.3	11.4	2.9	40.0	28.6	11.4	40.7	29.3	11.4
2002	21.4	14.8	6.6	44.3	32.8	11.5	42.6	30.3	12.3
1999	13.9	12.5	1.4	34.0	27.8	6.3	36.1	30.6	5.6

[a] Year of model prediction.

[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 suitable habitat when there was no actual nest observed. False negatives indicate the

percentage of the total error attributed to the model predicting unsuitable habitat when there actually was a nest observed. The combined percentages of false negatives and false positives equals 100% total error.

Table 7. Percentage of suitable nesting habitat and number of piping plover nests (*Charadrius melodus*) in 1999, 2002, and 2008 in 1-km subsections of Assateague Island nesting sites, MD and VA. Model predictions of nest site suitability were calculated for each 1-km section of Assateague Island as the percentage of all available sample points (5x5 m) that were suitable (p(suitable habitat)>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(suitable habitat)>0.5.

		Percentage of available points in a 1-km section of island where p(suitable habitat) > 0.5[c]										
Year[a]	Island region[b]	0–10	10–20	20–30	30–40	40–50	50–60	60–70	70–80	80–90	90–100	Total # nests
2008	North end	-	20	16	34	-	-	-	-	-	-	70
	OSV	1	1	-	-	-	-	-	-	-	-	2
	WB/ANA	7	3	-	-	20	-	-	-	-	-	10
	Overwash	-	6	-	-	-	-	-	-	-	-	6
	Hook	-	14	-	-	20	-	-	-	-	-	34
2002	North end	-	-	1	23	19	15	-	-	-	-	58
	OSV	-	3	-	-	-	-	-	-	-	-	3
	Overwash	-	-	5	-	-	-	7	-	-	-	12
	Hook	-	11	5	-	-	-	-	-	-	-	16
1999	North end	4	-	3	5	31	12	17	-	-	-	72
	OSV	2	-	-	-	-	-	-	-	-	-	2
	Overwash	-	-	6	-	-	-	-	-	-	-	6
	Hook	-	-	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] A (-) means zero island sections were predicted to fall in that range of available suitable points. We used a (-) instead of a (0) to facilitate ease of reading.

Table 8. Number of 1-km sections (out of 10 total sections) of the North end of Assateague Island, MD as characterized by the percentage of available suitable nesting sites (p(suitable habitat) > 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 models.

Year or scenario predicted [a]	0–10	10–20	20–30	30–40	40–50	50–60	60–70	70–80	80–90	90–100
2008	-	5	3	2	-	-	-	-	-	-
2002	1	1	1	4	2	1	-	-	-	-
1999	2	-	2	1	2	2	1	-	-	-
Future 3 mm SLR	-	-	-	-	3	3	2	2	-	-
Future 4.1 mm SLR	-	-	-	-	3	3	2	2	-	-
Future 3 mm SLR with SD	-	-	-	-	3	3	4	-	-	-
Future 3 mm SLR with FD	-	-	-	-	3	3	2	2	-	-
Future 4.1 mm SLR with SD	-	-	-	-	3	3	2	2	-	-

Future 4.1 mm SLR with FD	-	-	-	-	3	3	2	2	-	-

[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 percentage of all available points that were suitable (p(suitable habitat)>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(suitable habtiat>0.5. A (-) means zero island sections were predicted to fall in that range of available suitable points. We used a (-) instead of a (0) to facilitate ease of reading.

Table 9. Mean ±SD of probability values for suitable habitat (p(suitable habitat) > 0.5) for piping plovers (*Charadrius melodus*) in each 1-km section on the North End of Assateague Island, MD, for 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 a shoreline change, geomorphology, and piping plover models.

Island Section	3 mm SLR	3 mm SLR + SD	3 mm SLR + FD	4.1 mm SLR	4.1 mm SLR + SD	4.1 mm SLR + FD
1	0.60 (0.09)	0.59 (0.08)	0.60 (0.09)	0.59 (0.09)	0.59 (0.08)	0.60 (0.09)
2	0.62 (0.08)	0.61 (0.06)	0.62 (0.08)	0.62 (0.08)	0.61 (0.06)	0.62 (0.08)
3	0.64 (0.09)	0.63 (0.07)	0.64 (0.09)	0.64 (0.09)	0.63 (0.07)	0.64 (0.09)
4	0.65 (0.09)	0.63 (0.06)	0.65 (0.09)	0.65 (0.09)	0.63 (0.06)	0.65 (0.09)
5	0.62 (0.08)	0.62 (0.07)	0.62 (0.08)	0.62 (0.08)	0.62 (0.07)	0.62 (0.08)
6	0.60 (0.09)	0.60 (0.09)	0.60 (0.09)	0.60 (0.09)	0.60 (0.09)	0.60 (0.09)
7	0.61 (0.09)	0.60 (0.10)	0.61 (0.09)	0.61 (0.09)	0.60 (0.10)	0.61 (0.09)
8	0.61 (0.09)	0.60 (0.09)	0.61 (0.09)	0.61 (0.09)	0.60 (0.09)	0.61 (0.09)
9	0.60 (0.09)	0.59 (0.09)	0.60 (0.09)	0.60 (0.09)	0.59 (0.09)	0.60 (0.09)
10	0.58 (0.07)	0.59 (0.07)	0.58 (0.07)	0.58 (0.07)	0.59 (0.07)	0.58 (0.07)

Table 10. Percentage of points by 1-km sections of the North end of Assateague Island National Seashore, MD, that were categorized as sparse, herbaceous, or woody vegetation in 2008, and under future scenarios 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 models. All other scenarios (including a 4.1 mm/yr SLR, and management options of frequent, biannual, near-shore sand deposition (SD) and heavily-notched foredune (FD)) had the same percentage of points as the 3 mm/yr SLR scenario.

Island section	Sparse[a]			Herbaceous			Woody		
	2008	3mm/yr	3mm/yr with SD	2008	3mm/yr	3mm/yr with SD	2008	3mm/yr	3mm/yr with SD
43	36	72	52	24	2	15	16	7	12
44	49	96	54	31	1	21	13	3	24
45	44	52	45	40	0	5	11	0	2
46	36	67	64	48	13	14	11	4	5
47	33	62	65	41	27	23	19	4	4
48	34	77	76	49	12	12	12	7	8
49	33	77	71	49	9	15	13	8	7
50	32	58	55	49	19	23	17	11	11
51	31	46	41	54	15	21	13	12	10
52	16	100	76	48	0	24	33	0	0

[a] The 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.

Figures

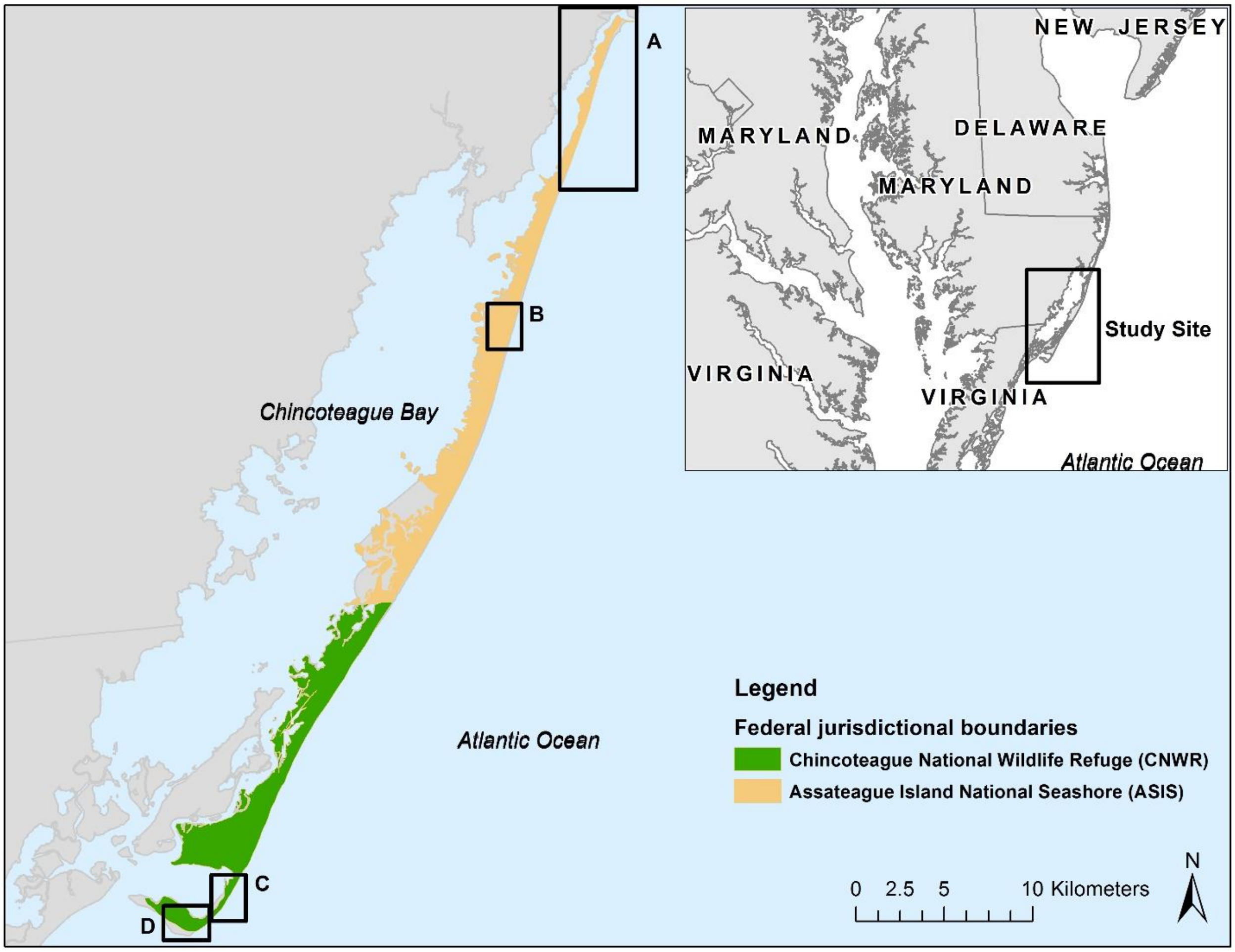


Fig. 1. We generated Piping Plover (*Charadrius melodus*) nesting probabilities using three linked models that considered shoreline change due to sea level rise (SLR) and storms, barrier island geomorphological variables and plover nesting habitat suitability. Initial models were developed with data 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.

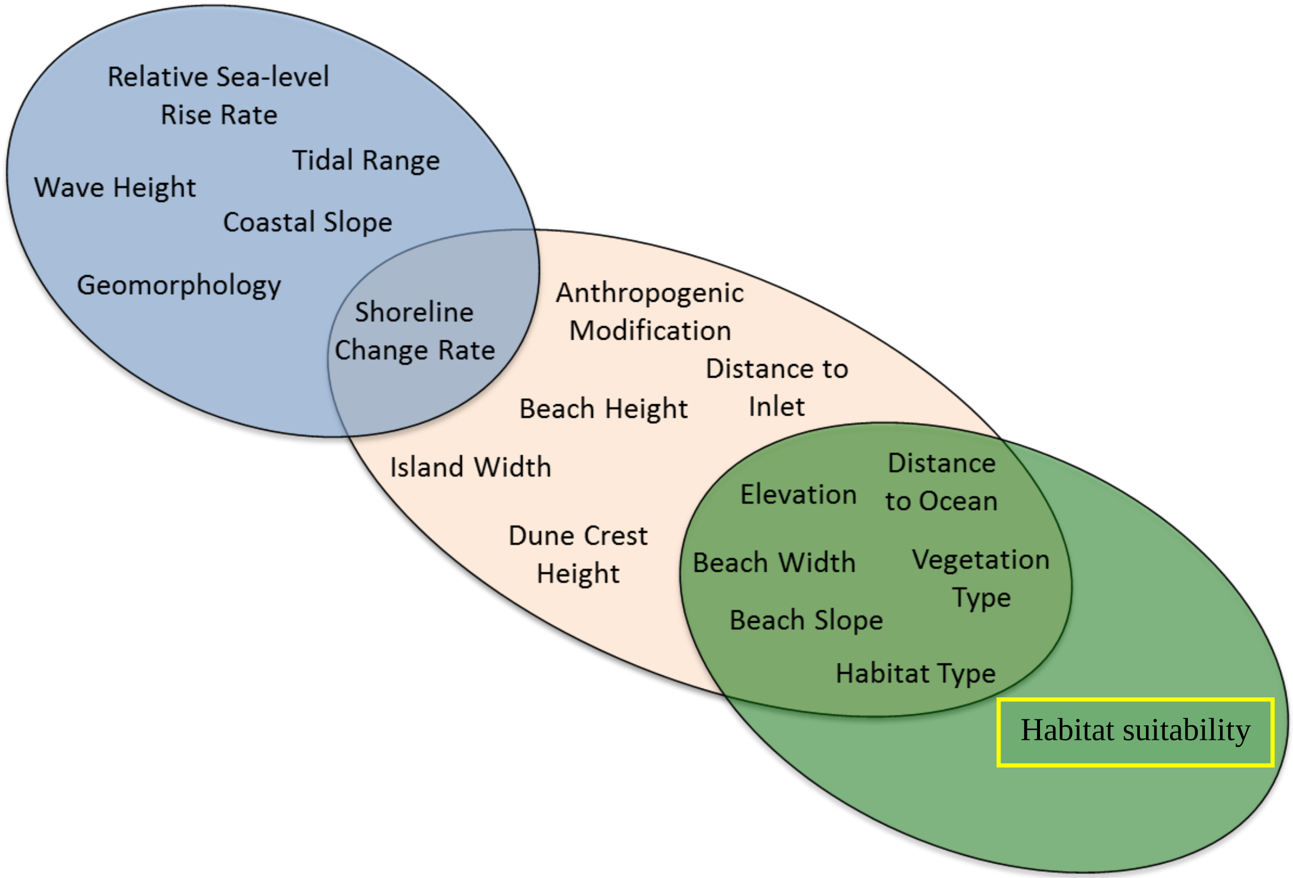


Figure 2. Schematic representation of three independent Bayesian Networks (BNs) constructed using Netica software (Norsys, 1992-2010) for 1) the shoreline change model (blue oval), 2) the geomorphology model (nude oval), and 3) the Piping Plover (*Charadrius melodus*) nest selection model (green oval). 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 suitable or unsuitable nesting habitat probability from this linked network is denoted by the habitat suitability variable outlined in yellow.

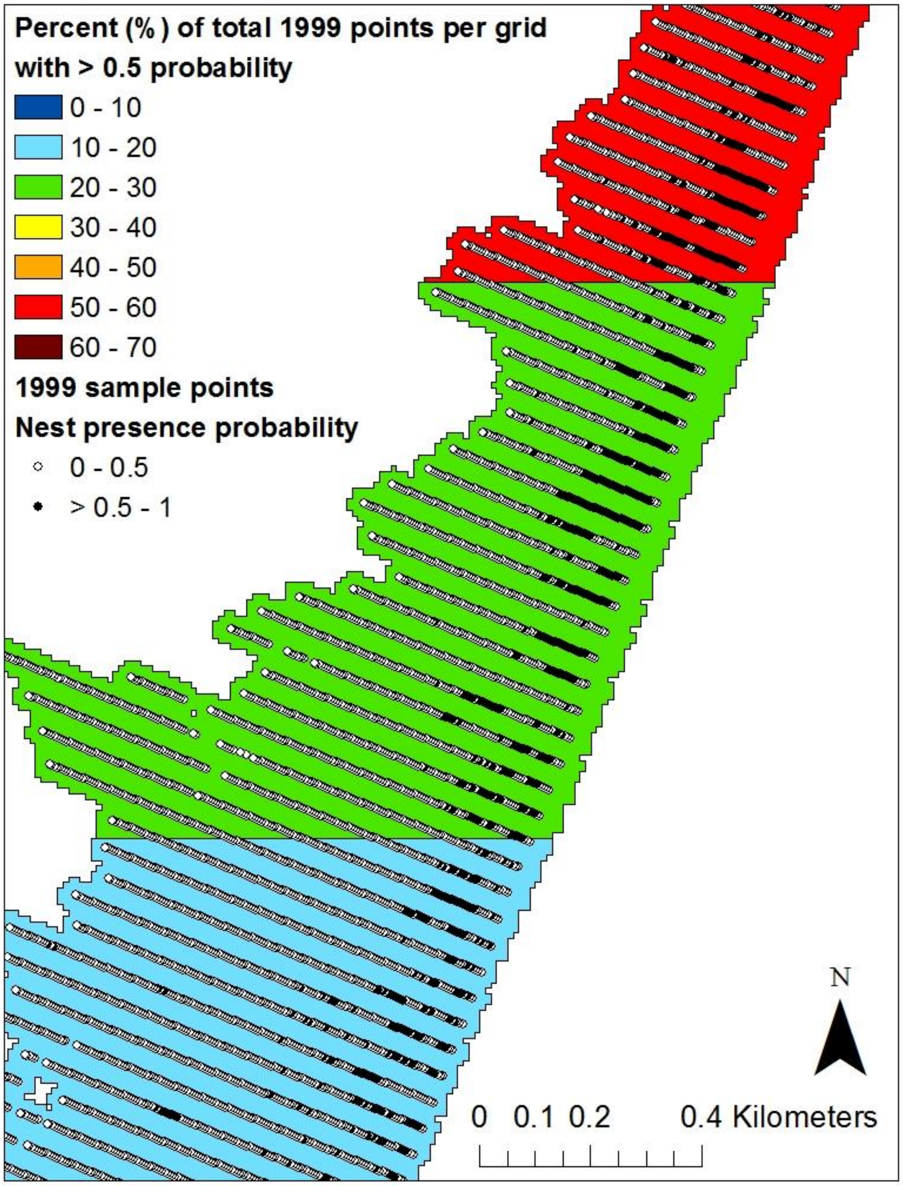


Figure 3. An example of the color-coded map developed to show the percent of total points with $p > 0.5$ predicted piping plover (*Charadrius melodus*) suitable nesting habitat probability within 1 km island sections of Assateague Island, MD and VA. The lines of dots illustrate points sampled every 5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

suitable habitat 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 $p > 0.5$ suitable habitat probability.

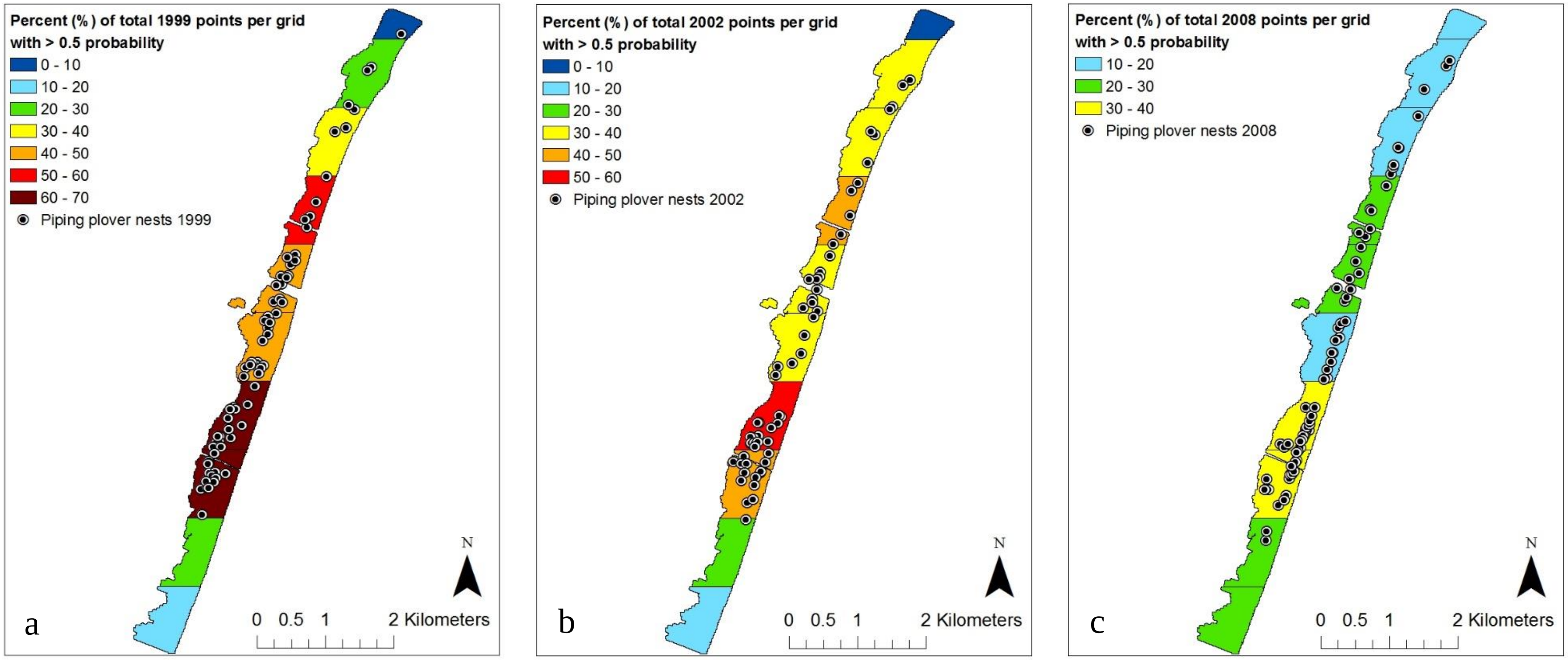
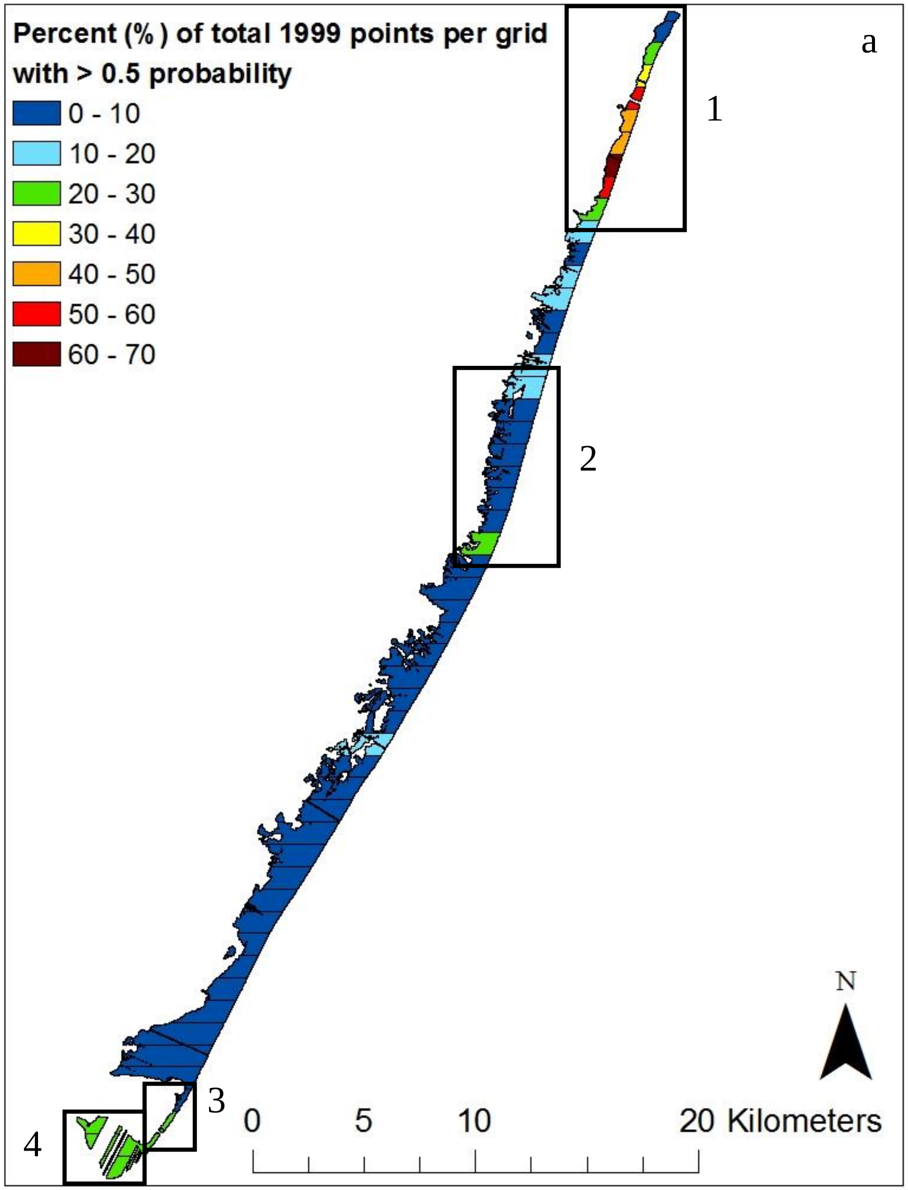
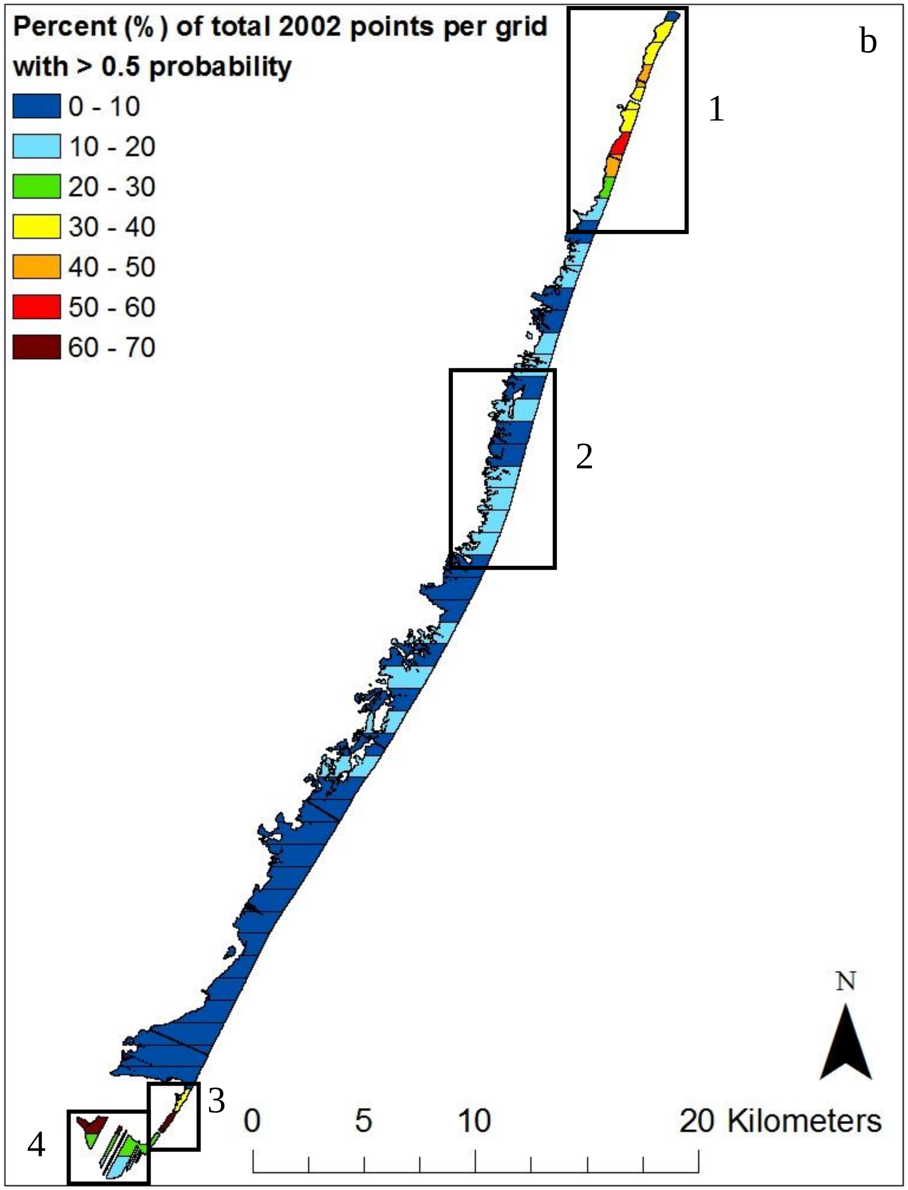


Figure 4. Percent of total points per 1 km island section with $p > 0.5$ predicted Piping Plover (*Charadrius melodus*) suitable nesting habitat probability for 1999 (a), 2002 (b), and 2008 (c) on the northern 10 km of Assateague Island, MD. Percent ranges for each grid are displayed in color and actual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


Percent (%) of total 1999 points per grid with > 0.5 probability
0 - 10
10 - 20
20 - 30
30 - 40
40 - 50
50 - 60
60 - 70
a
1
2
3
4
N
0
5
10
20 Kilometers


Percent (%) of total 2002 points per grid with > 0.5 probability
0 - 10
10 - 20
20 - 30
30 - 40
40 - 50
50 - 60
60 - 70
b
1
2
3
4
N
0
5
10
20 Kilometers

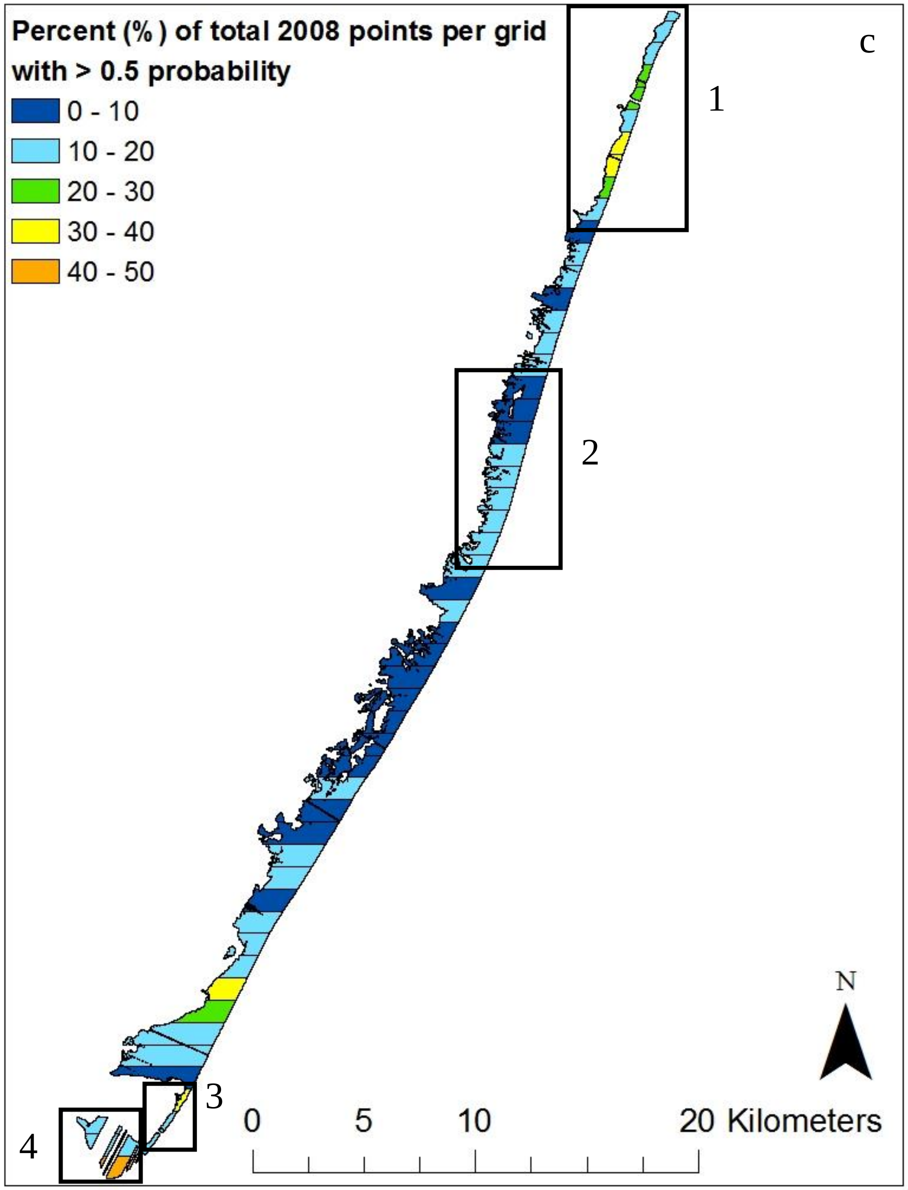

Percent (%) of total 2008 points per grid with > 0.5 probability
0 - 10
10 - 20
20 - 30
30 - 40
40 - 50
c
1
2
3
4
N
0
5
10
20 Kilometers

Figure 5. Percent of total points per 1 km island section with $p > 0.5$ predicted Piping Plover (*Charadrius melodus*) suitable nesting habitat probability for 1999 (a), 2002 (b), and 2008 (c) 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 (1) the northern 10 km of Assateague Island National Seashore, MD, (2) a portion of the over-sand vehicle zone of Assateague Island National Seashore and areas known as the (3) Overwash and (4) Hook at Chincoteague National Wildlife Refuge, VA.

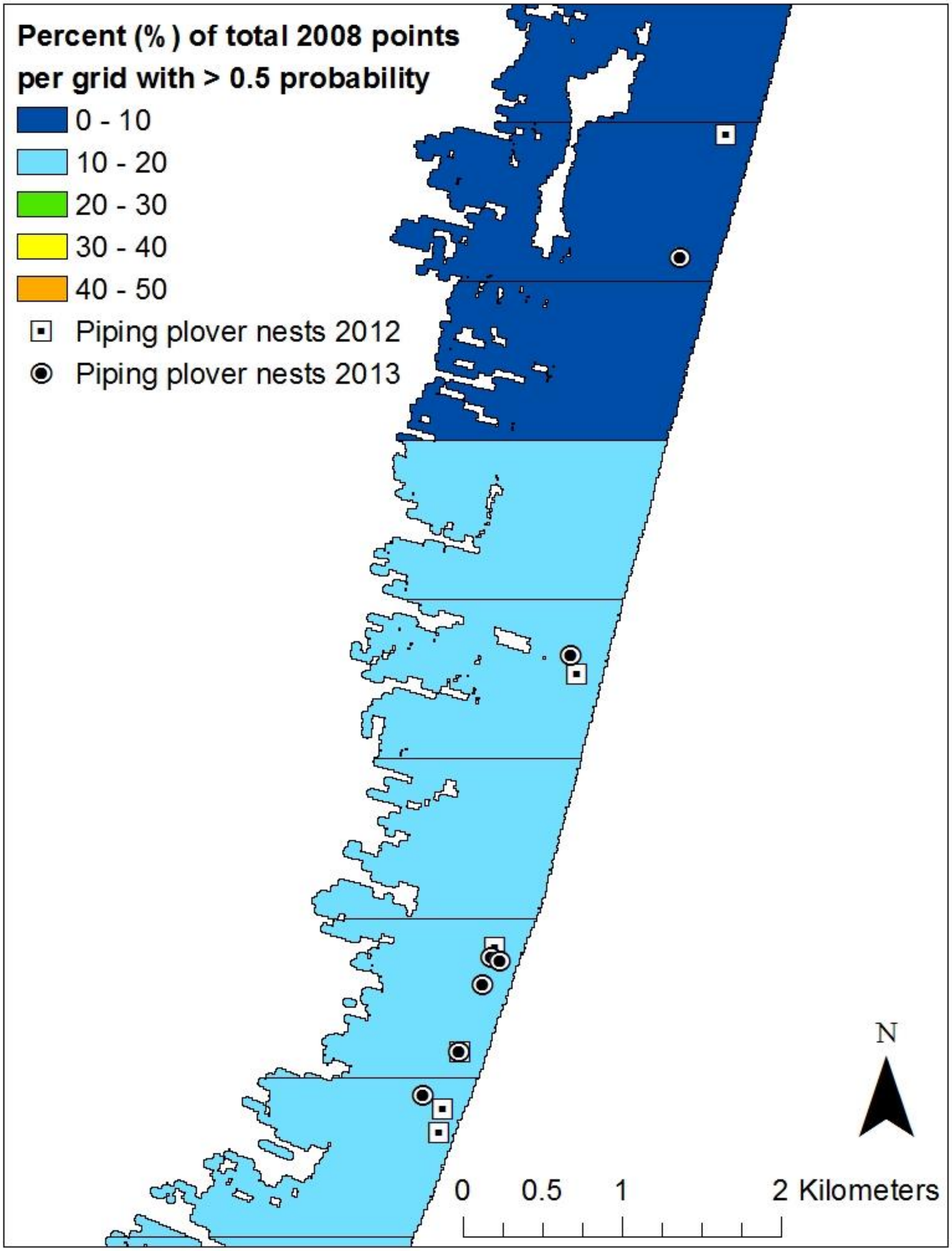
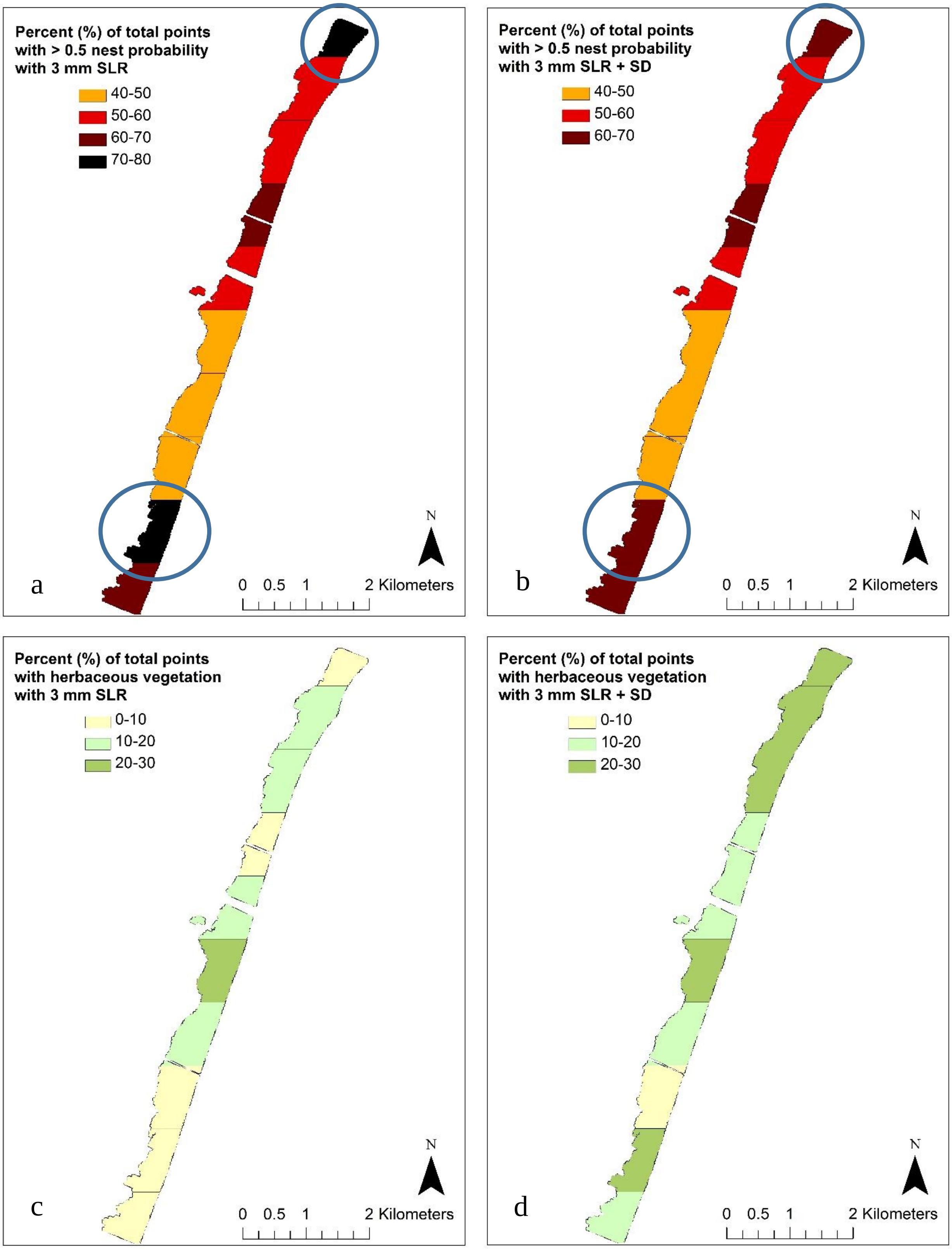

Percent (%) of total 2008 points per grid with > 0.5 probability
0 - 10
10 - 20
20 - 30
30 - 40
40 - 50
Piping plover nests 2012
Piping plover nests 2013
N
0
0.5
1
2 Kilometers

Figure 6. Percent of total points per 1 km section of island with $p > 0.5$ predicted Piping Plover (*Charadrius melodus*) suitable nesting habitat 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.


Percent (%) of total points with > 0.5 nest probability with 3 mm SLR
40-50
50-60
60-70
70-80
N
a
0 0.5 1 2 Kilometers
Percent (%) of total points with > 0.5 nest probability with 3 mm SLR + SD
40-50
50-60
60-70
N
b
0 0.5 1 2 Kilometers
Percent (%) of total points with herbaceous vegetation with 3 mm SLR
0-10
10-20
20-30
N
c
0 0.5 1 2 Kilometers
Percent (%) of total points with herbaceous vegetation with 3 mm SLR + SD
0-10
10-20
20-30
N
d
0 0.5 1 2 Kilometers

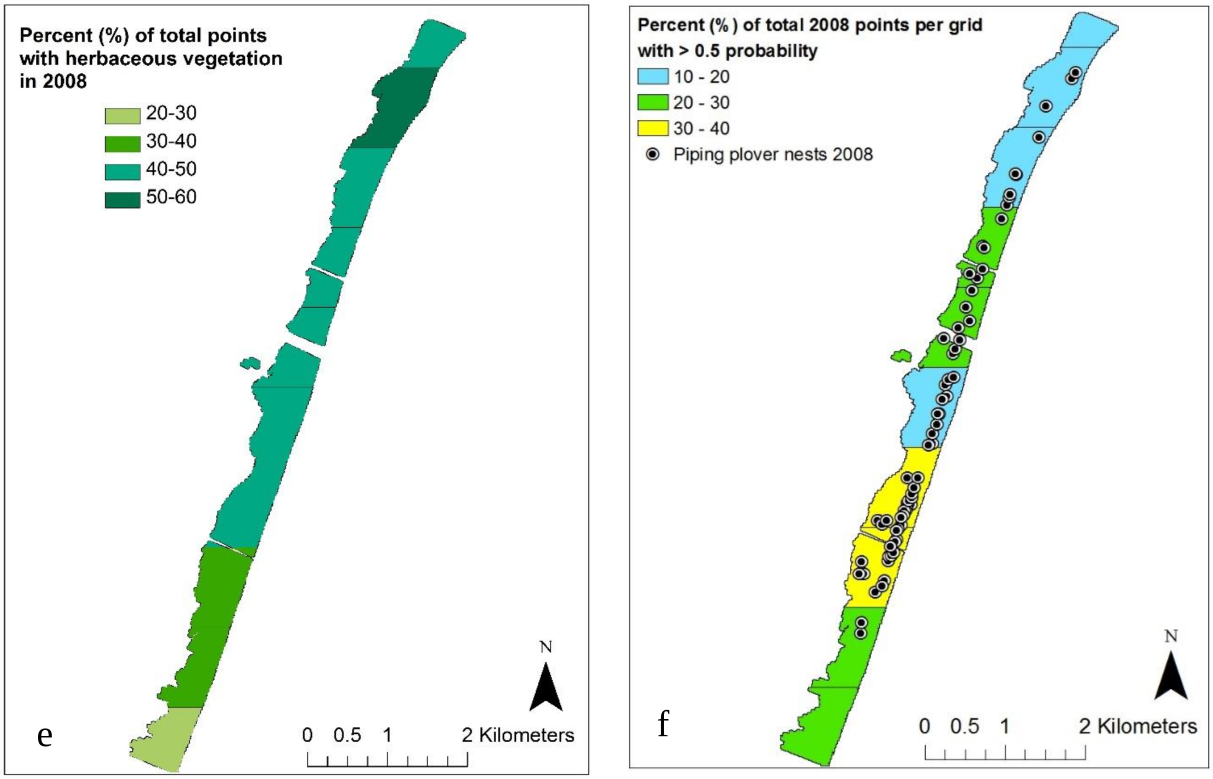


Figure 7. Percent of total points per 1 km length grid with > 0.5 predicted Piping Plover (*Charadrius melodus*) suitable nesting habitat probability approximately 50-100 years in the future on the northern 10 km of Assateague Island, MD, under a) 3 mm/year sea-level rise and b) 3 mm/yr sea-level rise 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 c and d show corresponding percent (%) of total points within each grid that had herbaceous vegetation type (i.e. vegetation density >20% within minimum 25 m^2) under c) 3 mm/yr sea-level rise d) 3 mm/yr sea-level rise and a management strategy of frequent sand deposition along the entire North End. Plate e shows percent (%) of total points within each grid that had herbaceous vegetation type (i.e. vegetation density >20% within minimum 25 m^2) in 2008 and Plate f shows percent of total points per 1 km length grid with >

0.5 predicted Piping Plover (*Charadrius melodus*) suitable nesting habitat probability in the same year.

Appendices

Appendix 1. Description of the method used to compare hindcasting predictions of piping plover (*Charadrius melodus*) habitat suitability for 1999, 2002, and 2008, using a simple and complete version of a piping plover habitat suitability model at Assateague Island, MD.

Objective: To compare predicted piping plover (*Charadrius melodus*) suitable nesting habitat probability for a complete and simple version of a piping plover habitat suitability model for 2008 on Assateague Island, MD and VA in order to decide the best version of the 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 A.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 A.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 models by developing hindcasting predictions of suitable nesting habitat using both the complete and simple version of a plover 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 suitable nesting habitat. 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 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(suitable habitat) > 0.5, then it was color-coded 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 plover model had a much lower overall percent of total points per 1 km island section with > 0.5 predicted piping plover (*Charadrius melodus*) suitable habitat probability compared to the simple model version (Figure A.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 suitable habitat. The remaining 4 island sections had 10-20% of points within each island section with a > 0.5 probability of suitable habitat. 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 suitable habitat (Table A.1). Percentages of points within each island section with a > 0.5 probability of suitable habitat ranged up to 30-40% with the simple model. A majority of this increase suitable habitat 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 suitable habitat. 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 suitable habitat 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 suitable habitat. Furthermore, the simple model predictions also showed higher percentages of points within each island section with a > 0.5 probability of suitable habitat 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 A.2).

Conclusions

Overall, the complete model habitat suitability 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 suitable habitat. The simple model suitable habitat 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 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 A.1. Number of 1-km sections (out of 53 total sections) of Assateague Island, MD as characterized by the percentage of available suitable nesting sites (p(suitable habitat) > 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 habitat suitability model. The predicted output is based on linking a shoreline change, geomorphology, and plover models.

Year[a]	Island Region[b]	Proportion of available points in a 1-km section of island where p(nest presence) > 0.5b										
		0 – 10	10-20	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 percentage of all available points that were suitable (p(suitable habitat)>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(suitable habitat)>0.5. A (-) means no island sections were predicted to fall in that range of available suitable points.

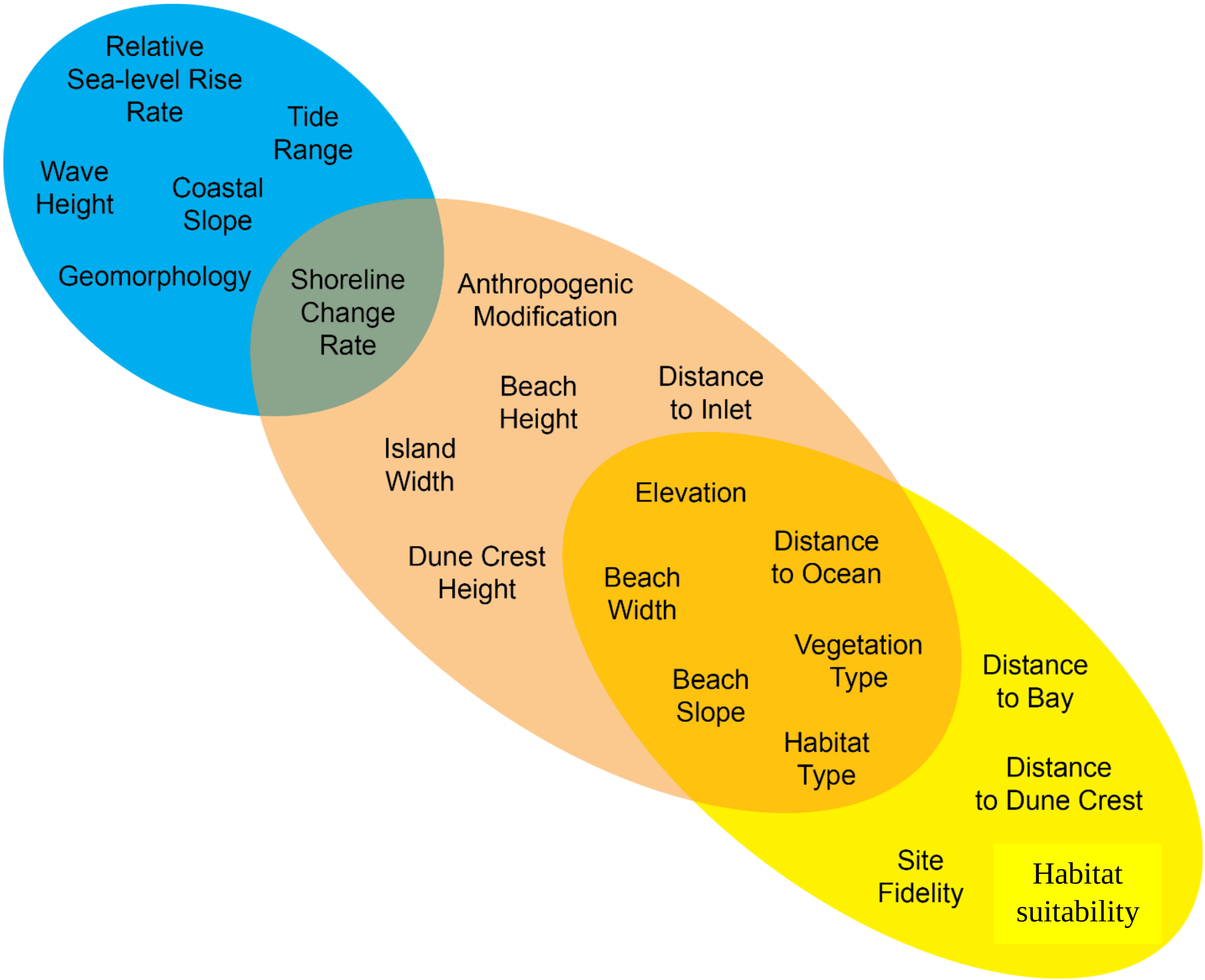


Figure A.1. Schematic representation of three independent Bayesian Networks (BNs) constructed using Netica software (Norsys, 1992-2010) for 1) the shoreline change model (blue oval), 2) the geomorphology model (orange oval), and 3) the complete piping plover (*Charadrius melodus*) habitat suitability model (yellow oval). The simple version of the plover 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 plover model were linked through several shared variables (denoted by overlapping orange-yellow area).

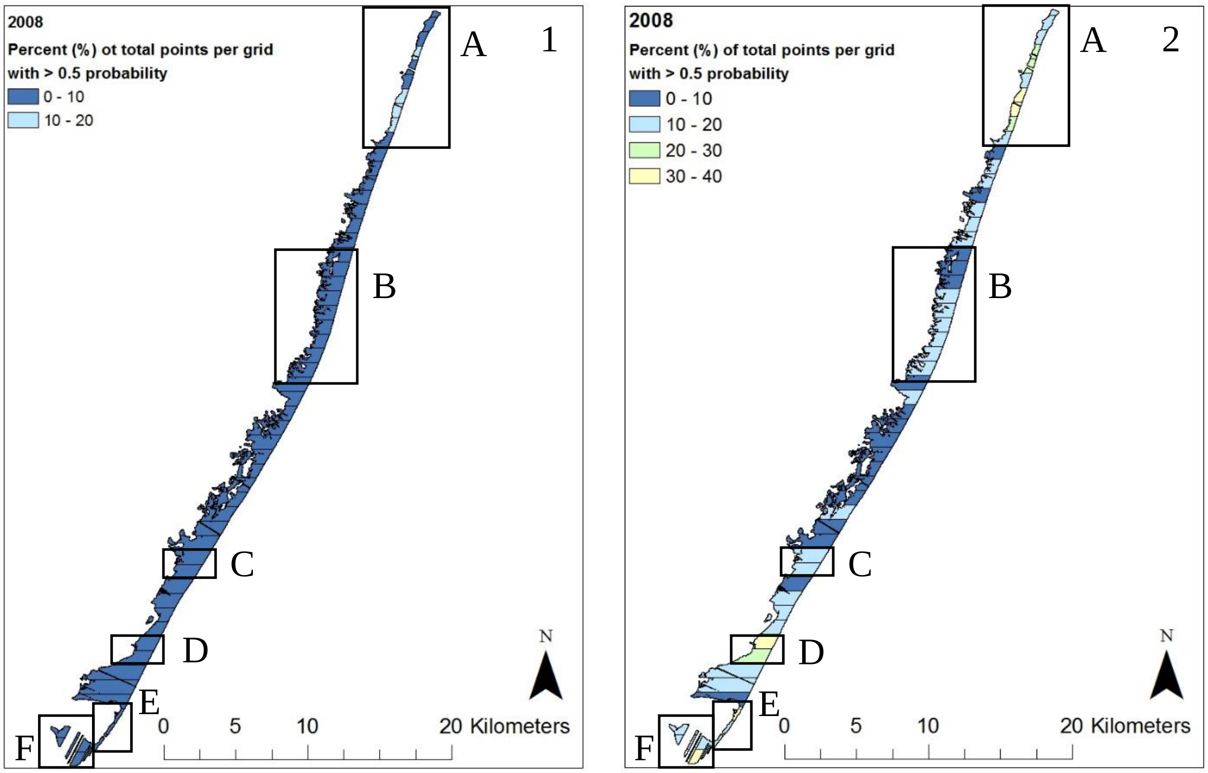


Figure A.2. Percent of total points per 1 km length grid with > 0.5 predicted piping plover (*Charadrius melodus*) suitable nesting habitat probability for a complete (1) and simple (2) version of a piping plover habitat suitability model for 2008 on Assateague Island, MD and VA. Percent ranges for each 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 2. Number of 1-km sections (out of 53 total sections) of Assateague Island, VA and MD as characterized by the percentage of available suitable nesting sites (p(suitable habitat) > 0.5) for piping plovers (*Charadrius melodus*) in each 1-km section for past conditions in 1999, 2002, and 2008 .

Year Predicted [a]	0–10	10–20	20–30	30–40	40–50	50–60	60–70	70–80	80–90	90–100
1999	35	6	6	1	2	2	1	-	-	-
2002	27	15	2	5	2	1	1	-	-	-
2008	17	27	4	4	1	-	-	-	-	-

[a] Year of model predictions.

[b] Model predictions of nest site suitability were calculated for each 1-km section of Assateague Island as the percentage of all available points that were suitable (p(suitable habitat)>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(suitable habitat)>0.5. A (-) means no island sections were predicted to fall in that range of available suitable points.

Appendix 3. Error rates (percentage of predictions that fell outside of the observed input bin values, %) for geomorphology variables elevation, beach slope, habitat type, and vegetation type computed at piping plover (*Charadrius melodus*) nest and random point locations using a geomorphology Bayesian network based on three years of data from Assateague Island National Seashore, MD, USA.

Variable[a]	Year[b]	Overall Error Rate (%)	Correct Predictions Error Rate (%)[c]	Incorrect Predictions Error Rate (%)
Elevation (m)	1999	34	34	35
	2002	34	34	35
	2008	37	39	34
Beach slope (%)	1999	31	26	59
	2002	49	50	52
	2008	54	57	50
Habitat type	1999	26	25	27
	2002	28	31	24
	2008	20	17	25
Vegetation type	1999	74	78	67
	2002	43	49	35
	2008	46	42	54

[a] "Elevation (m)" is the vertical height above sea-level of a nest or random point without nest; "Beach slope (%)" is the average rise over run within a 5 m radius of a nest or random point without nest; "Vegetation type" is the general type and density of vegetation at a nest or random point without nest; "Habitat type" is the general habitat type at the nest or random point without nest.

[b] Year of model prediction.

[c] Correct predictions represent predictions of suitable nesting habitat that accurately reflected the presence of an actual nest in the data, incorrect predictions did not.

Appendix 4. Error rates (percentage of predictions that fell outside of the observed input bin values, %) for geomorphology variables elevation, beach slope, habitat type, and vegetation type computed at piping plover (*Charadrius melodus*) nest and random point locations using a linked geomorphology and piping plover Bayesian network based on three years of data from Assateague Island National Seashore, MD, USA.

Variable[a]	Year[b]	Overall Error Rate	Correct Predictions Error Rate[c]	Incorrect Predictions Error Rate
Elevation (m)	1999	34	33	37
	2002	38	39	37
	2008	37	40	33
Beach slope (%)	1999	31	27	39
	2002	49	50	48
	2008	54	58	49
Habitat type	1999	26	24	31
	2002	38	37	38
	2008	21	18	26
Vegetation type	1999	74	78	67
	2002	44	46	42
	2008	48	42	56

[a] "Elevation (m)" is the vertical height above sea-level of a nest or random point without nest; "Beach slope (%)" is the average rise over run within a 5 m radius of a nest or random point without nest; "Vegetation type" is the general type and density of vegetation at a nest or random point without nest; "Habitat type" is the general habitat type at the nest or random point without nest.

[b] Year of model prediction.

[c] Correct predictions represent predictions of suitable nesting habitat that accurately reflected the presence of an actual nest in the data, incorrect predictions did not.

CHAPTER 4

RED FOX (*VULPES VULPES*) OCCUPANCY AND HABITAT USE ON ASSATEAGUE ISLAND NATIONAL SEASHORE, MARYLAND

Abstract

Effective predator management is a key component of shorebird conservation, along with co-management of other threats such as habitat change and human disturbance. On the U.S. Atlantic Coast, high rates of human development have been associated with increases in shorebird predators, especially red foxes (*Vulpes vulpes*), raccoons (*Procyon lotor*), striped skunks (*Mephitis mephitis*), and Virginia opossums (*Didelphis virginiana*). Extensive human and financial resources are allocated to protecting shorebirds of conservation concern from predators, most notably for the federally-threatened piping plover (*Charadrius melodus*), including a variety of predator control mechanisms such as nest exclosures and predator removal programs. However, little is known about the effectiveness of this predator management because predator population ecology and behavior in coastal habitats in general, and on barrier islands in particular, are poorly understood. We examined occupancy and habitat use of the red fox, an important shorebird predator on the U.S. Atlantic Coast, on Assateague Island National Seashore, MD from 2012-2014. Using camera trap surveys across 3 grids located near and around piping plover nesting areas, we found that red fox occupancy was strongly tied to eastern cottontail (*Sylvilagus floridanus*) trap success, increasing sharply with increased eastern cottontail trap success. We also found that red fox occupancy did not change in response to an intensive eradication program on the northern section of the island. More detailed studies of the strong connection of red fox to eastern cottontails in coastal landscapes, and of individual fox

movement before and after lethal removal efforts, may provide important insights into effective predator control.

Introduction

Predator management is an integral aspect of shorebird conservation, particularly for threatened and imperiled species such as the piping plovers (*Charadrius melodus*), American oystercatchers (*Haematopus palliatus*), and least terns (*Sternula antillarum*) (USFWS 1985; Rimmer and Deblinger 1992; Davis et al. 2001). Though shorebirds have evolved many defense mechanisms against predators (Gochfeld 1984), a suspected increase in shorebird nest and chick predation, combined with other increasing threats such as habitat loss and disturbance, have made predator management a key part of recovery plans for imperiled shorebird species (USFWS 1996; Schulte et al. 2007; Cohen et al. 2009; USFWS 2013). Furthermore, human development and associated habitat change have been linked to expansions in the populations and ranges of mammalian mesocarnivores, such as red foxes *(Vulpes vulpes)*, raccoons *(Procyon lotor*), striped skunks *(Mephitis mephitis)*, and Virginia opossums *(Didelphis virginiana)* (Reynolds and Tapper 1996; Evans 2004). On the U.S. Atlantic Coast, beach development and high levels of human recreation have occurred concurrently with the proliferation of these predators (Strauss 1990; Lauro and Tanacredi 2002).

The piping plover is a shorebird that was listed as threatened along its U.S. Atlantic Coast breeding range under the Endangered Species Act in 1986 (USFWS 1985). Predators negatively impact piping plover productivity in some locations along the coast (MacIvor et al. 1990; Strauss 1990; Patterson et al. 1991; Houghton 2005; Cohen et al. 2009), with red fox and raccoon being frequent predators (MacIvor et al. 1990; Melvin et al. 1992; Patterson et al. 1991; Doherty and Heath 2011). Consequently, these predators are heavily managed on a number of U.S. Atlantic coast beaches, an endeavor that can constitute a significant portion of the yearly shorebird conservation efforts. For example, predator monitoring, research, and control in Massachusetts alone costs hundreds of thousands of US dollars a year (Clark and Niles 2000).

Despite significant effort and cost, the effectiveness of many predator control programs is questioned because predator effects on piping plovers and predator ecology on the U.S. Atlantic coast are poorly understood. Human expansion and development have altered the habitat along our coasts such that it is increasingly suitable for many predator species, thereby changing their historic distributions and habitat use, while also changing habitat suitability for nesting shorebirds. Current predator management techniques, such as predator exclosures, electric fencing, and lethal removal in coastal habitats are largely informed by trial and error methods, with little prior knowledge of site-specific predator population ecology and habitat use.

The few studies of mammalian predators in U.S. coastal habitats have focused on raccoons, and to a lesser extent on red fox. Parsons et al. (2013) found that raccoons primarily used salt marsh habitat on the Outer Banks in NC and that shorebird and turtle eggs on the ocean-fronting beach were sought out by a small number of raccoons. Erwin et al. (2001) noted a marked increase in the range extent of raccoon and red fox on barrier islands in VA from historic extent. Porter et al. (2015) found that red fox are more likely to move onto Virginia barrier islands from the mainland, whereas raccoons are more likely to move onto islands from other nearby islands. However, Dueser et al. (2013) found that inter-island movements by raccoons are infrequent events. Finally, O’Connell et al. (2006) estimated occupancy and detection of 10 mammal species (including red fox, raccoon, Virginia opossum, and striped skunks) on Cape Cod National Seashore, Massachusetts, to compare methods for estimating predator population parameters in coastal areas.

Current predator management techniques such as protecting nests with exclosures have been questioned because exclosures do not always translate into higher shorebird breeding productivity (Pauliny et al. 2008) and have occasionally attracted predators such as red fox that can cue in to nest locations using the conspicuous nest exclosure structures (NPS 2007-2014; Beaulieu et al. 2014), causing nest abandonment (Murphy et al. 2003, Roche et al. 2010) and adult mortality (Vaske et al. 1994, USFWS 1996). Furthermore, predator removal programs are controversial because their effectiveness against nest and chick predation is not well understood (Hecht et al. 2014) and can be costly. For example, the Atlantic Flyway Shorebird Business Strategy outlines a funding gap of 9.5 million USD to implement predator management programs for American oystercatchers, piping plovers, snowy plovers (*Charadrius nivosus*), and Wilson's plovers (*Charadrius wilsonia*; Winn et al. 2015).

A better understanding of mammalian predator population ecology is greatly needed to increase the effectiveness of predator management for shorebird conservation. Specifically, more information on key shorebird predator occurrence in varied coastal habitats and habitat factors influencing their occurrence would provide baseline knowledge to understand how various predator management techniques may affect predators and their prey. In order to address this need, we used camera traps to quantify red fox occupancy and habitat factors affecting red fox occupancy, as foxes are a key shorebird predator on Assateague Island National Seashore, MD (Patterson et al. 1991; NPS 2007-2014). The red fox is one of the most studied carnivores in North America (Ables 1975) but wide variations in its diet, habitat use, spatial movement, and sociality combined with a lack of studies in coastal habitats make it difficult to draw valid conclusions about red fox ecology on barrier islands. To our knowledge, there are no previous studies that have estimated specific population parameters such as occupancy and detection of red foxes on barrier islands or in coastal habitat along the U.S. Atlantic Coast. O'Connell et al. (2006) did estimate red fox occupancy in Cape Cod Massachusetts but these estimates likely do not reflect true occupancy and detection because the sampling design was not designed specifically for red fox, nor did it associate red fox occupancy with habitat use or movement patterns.

Other population ecology studies of red fox have been conducted in coastal habitats in Europe, but these habitats differ from those on the U.S. Atlantic Coast in their mesopredator and prey assemblages, weather patterns, exposure to major forces of change such as sea-level rise, habitat diversity, geomorphology, and the absence of barrier islands (a key component shaping coastal ecosystems on the U.S. East Coast; Calisti et al. 1990; Cavallini and Lovari 1994; Dekker et al. 2001; Sarmento et al. 2009). Wide variations in red fox ecology make it difficult to extend conclusions from these European studies to red fox on the U.S. East Coast. Thus, our objectives in this study were to estimate occupancy and detection for red foxes on a barrier island in MD, identify the covariates (year, season, camera grid, landscape level habitat, co-occurring prey and predator species, and large ungulate species) that have the largest effect on red fox occupancy, and assess potential differences in occupancy among individual camera grids, seasons, and years. Finally, we used these results to assess the effect of lethal fox removal on their occupancy.

Methods

Study site

Assateague Island is a 58-km barrier island off the coasts of Maryland and Virginia, U.S. (Fig. 1). The National Park Service (NPS) manages Assateague Island National Seashore (ASIS) on most of the Maryland portion, except for a small portion managed by the state of Maryland as Assateague State Park; our study was conducted with the national seashore boundaries.

Assateague Island National Seashore's habitats include bayside tidal marshes and mudflats, interior pine dominated coniferous, deciduous shrub, and ocean-fronting dunes and sandy beaches that include overwash fans (open flat low elevation areas resulting from water overwashing during severe storms and high tide events; Morton et al. 2007).

Imperiled shorebirds such as piping plovers, American oystercatchers (a species of concern in MD), and least terns (a state-threatened species), nest at ASIS (Schupp et al. 2013) and face depredation threats from a number of predators, particularly red foxes. The majority of piping plover nests at ASIS are on the northern 10 km of the island known as the North End, and a smaller number of nests are located in the over sand vehicle (OSV) zone south of the North End. ASIS has protected all located piping plover nests with predator exclosures every year since at least 1991. In 2008, an adult red fox on the North End learned to access protected nests by jumping on top of exclosures, caving in the netting on top. This fox behavior was thought to be a main cause for the high nest failure (60%) in that year, as fox tracks were found inside damaged exclosures and around nests that had been destroyed or abandoned. Smaller fox tracks were also seen, indicating that fox kits were also learning this behavior. Concern for plover nest success after this event prompted ASIS staff to employ USDA APHIS to lethally remove all encountered red fox, and occasionally raccoon, on the North End in 2009 and every year thereafter. This lethal removal occurred during this study period in 2013 and 2014 between our winter and spring seasons (ASIS 2011).

Photographic sampling design

We deployed camera traps at three locations on ASIS; one on the northern 10 km of the island known as the North End (grid A), and two more in the over sand vehicle (OSV, grids B and C) zone at ASIS (Fig. 1, see Appendix S1-S2). The areas sampled (the North End and OZV zone) were selected as they include the major piping plover nesting areas on ASIS (NPS 2011); we chose these grid locations to be in proximity to piping plover nest areas so that we could assess red fox occupancy and habitat use within and around actual nesting sites.

We designed the spacing of our cameras to best sample red fox occupancy, based on what was known about red fox movements from other studies. Appropriate camera spacing is an important consideration as it can significantly affect estimations of occupancy and population parameters (Stickel 1954; Tanaka 1980; Wegge et al. 2004; Dillon and Kelly 2007). Cameras should be spaced to maximize capture probability for the study target species. Dillon and Kelly (2007) recommend including at least two camera traps per average home range size. However, red fox home range size is highly variable, ranging from 10-5000 ha (Macdonald 1987; Voigt 1987), making an average home range size unreliable. Instead, we used the diameter of the smallest home range size to maximize capture probability for the red fox (see Sarmento et al. 2009 for a similar camera spacing methodology for red fox). Therefore, while we generally placed cameras within each habitat type along well established wildlife trails when present, we maintained a minimum spacing of approximately 300 m (±25 m) between each camera station to best accommodate sampling for the red fox (see Appendix S1 for specific UTM locations of individual camera stations for each grid).

Cameras were set up in spring (April to June), fall (August to October), and winter (January to March) from 2012-2014. There were 25 cameras each in the two camera grids in the OSV zone (grids B and C) that operated for approximately 43 days in each season and year. We staggered the timing of these two grids with the North End grid A. Grid A on the North End operated from mid-April to mid-May (spring), from mid-September to mid-October (fall), and from mid-Jan to mid-Feb (winter), and had 36 camera stations that operated for approximately

30 days each season and year. Grid A was not set up until the fall season in 2012, and therefore no data was recorded for this grid in spring 2012 (see Appendix S3 and S4 for specific dates and numbers of cameras).

Each camera station operated 24h/day and consisted of only one camera to maximize the number of sampling stations per habitat type (see Appendix S1). We did not have any cameras set up on sandy oceanfront beach because of a high flood risk, but cameras were set up in every other habitat type (marsh, pine forest, deciduous shrub, dunes, and overwash). We used Reconyx PC90 professional covert infrared cameras (Reconyx, Inc., Holmen, Wisconsin, USA) placed approximately 20 cm above the ground and attached to a metal pole sunk into the sand (Appendix S5). Each camera was checked every 10–14 days to ensure they were functioning properly and replace batteries, and memory cards as needed. Photographs were catalogued for analysis by the date and time of day recorded on each photograph.

Data analyses

We used a landscape occupancy model to investigate how habitat variables affected the probability of red fox occupancy and detection across ASIS. We compiled presence (1), absence (0) data to create capture histories of red fox for every 24-hour period in spring (n = 6), fall (n = 7), and winter (n = 7) surveys at all three camera grids (n = 20 capture histories total; see Appendix S4). We defined each 24-hour period that a camera was functioning properly as a trap night. To improve model convergence we collapsed these capture histories by one fifth of the original survey period. For example, if there were 50 total trap nights for a particular grid, we collapsed every 10 trap nights into one to create 5 total trap periods. We analyzed these capture histories in program PRESENCE (Patuxent Wildlife Research Centre, USGS, Maryland, USA;

Hines 2006) to provide an estimate of red fox occurrence and detection while accounting for spatial variation and variation in detection probability (Bailey et al. 2004).

We used the following variables as covariates in occupancy modeling to determine their influence on occupancy and detection of red fox: year, season, grid, macrohabitat type (marsh, pine forest, deciduous shrub, dunes, and overwash), sika deer (*Cervus nippon*) trap success (TS), white-tailed deer (*Odocoileus virginianus*) TS, feral horse (*Equus ferus caballus*) TS, raccoon TS, eastern cottontail (*Sylvilagus floridanus*) TS, human TS, and distance to nearest paved road. TS was used as an index of co-occurring species activity and was calculated by dividing the total number of capture events of each species by the number of trap nights at each camera station multiplied by 100. All captures of a given species within a 30 minute period were counted as one capture event and a trap night was defined as a 24 h period when the camera at a given station was functioning. We normalized all covariates within program PRESENCE, to achieve adequate model convergence.

We developed a priori models for landscape occupancy analysis and used Akaike Information Criterion, corrected for small sample sizes (AICc), to rank models (Akaike 1973). We did not use model-averaging because of a lack of competing models (top ranking model for each analysis had model weight of ≥ 0.90 and delta AIC < 2; see Appendix S6). We assessed goodness of fit for the most heavily parameterized model using Pearson's goodness-of-fit test ($P = 0.05$) and evaluated over-dispersion using the c-hat value (< 3.0). Finally, we modeled the occupancy and detection of species whose trap success was incorporated in the top models to compare habitat covariates for these species to those found for red fox.

Results

Our surveys resulted in a total of 22,628 trap nights (mean = 7,543 ± 620 SD per camera grid) and provided a total of 37, 399 photographic captures of mammals, from which we identified 11 species, including 4 carnivores (raccoon, red fox, North American river otter (*Lontra canadensis*), Virginia opossum; see Appendix S4).

We found no effect of grid, year, or season on red fox occupancy or detection (Figures 2-3, Appendix S6). Our finding of no effect of season on red fox occupancy included all cross-season and cross-year comparisons, including in Grid A where targeted red fox removal occurred between winter and spring seasons each year from 2012-2014.

Red fox landscape mean (± SE) occupancy was 0.43 ± 0.04 with a landscape detection of 0.26 ± 0.02. We found that macrohabitat was related to fox detection, whereas eastern cottontail TS was correlated most strongly with red fox occupancy (Table 1). Red foxes were detected most in dune habitats (P = 0.32 ± 0.02), followed by shrub (0.28 ± 0.02), marsh (0.23 ± 0.02), forest (0.20 ± 0.02), and overwash (0.16 ± 0.02; Figure 4). We found a strong positive relationship between red fox occupancy and eastern cottontail trap success (β= 0.42 ± 0.16; Figure 5). Thus, higher red fox occupancy was associated with higher eastern cottontail trap success.

We modeled occupancy of eastern cottontails, as trap success of this species was in the top model for red fox occupancy. Eastern cottontails occupied a little more than half the camera survey stations at ASIS (Ψ = 0.56 ± 0.03) and were also detected at a little more than half the camera stations (P = 0.56 ± 0.06). This detection was not uniform across camera grids or the landscape, yet none of the covariates tested were in the top model explaining cottontail occupancy and detection. The top model had two groups, this is a standard predefined model in PRESENCE that indicates that there was a difference among grids that the model detected with different occupancy estimates. Detection probability was also grid-specific, indicating that detection varied with each camera station (see Appendix S7).

Discussion

This is the first dedicated study of red fox occupancy and habitat use in a barrier island landscape. The only other study that estimated red fox occupancy in a habitat similar to our barrier island study system found a red fox occupancy of 0.35 ± 0.17 SE using camera traps on Cape Cod, MA (O'Connell et al. 2006); this estimate was slightly lower than our landscape occupancy estimate of 0.43 (±0.04 SE) at Assateague Island National Seashore. However, red fox detection in O'Connell et al. (2006) was only 0.15±0.09 SE compared to our estimate of 0.26±0.02 SE. The study by O'Connell et al. (2006) on Cape Cod, MA was focused on comparing occupancy sampling techniques, namely camera-trapping versus other sign, and thus camera spacing was not specifically designed to capture red fox. To avoid biasing the results of their survey technique comparison, cameras were separated by > 1 km to ensure the same individual was not detected at multiple sites so. Thus although their red fox occupancy estimates were useful in comparing different sampling techniques across multiple mammalian predators they likely were not representative of true red fox occupancy because the wide camera spacing likely did not capture all red fox given prior estimates of home range sizes (based on 300 m separation between cameras) and movements documented on Assateague Island National Seashore in this study (see Ch.4).

Although not as low as O'Connell et al. (2006), the low detection for red fox in this study demonstrates the cryptic nature of this species that is known to be difficult to detect (Mahon et al. 1998). Our findings that red fox detection was associated with macrohabitat was not surprising given our anecdotal observations of patterns of red fox tracks at Assateague Island

National Seashore. We most frequently observed red fox tracks along dune boundaries (i.e., they stay close to the base of the dunes) and along well-established wildlife trails in thick deciduous shrub habitat. In more open habitat, such as pine forest and overwash fans, red fox tracks that we encountered tended to wander. Given these observations, we were not surprised to find that red fox detection was highest in dune habitats, followed by shrub, marsh, forest, and overwash. In dune habitats, most of the cameras were placed fairly close to the dune line to avoid flooding and tampering by the public. In shrub and marsh habitats, cameras were place along wildlife trails because the vegetation was too thick to place them in other areas. Finally, in forest and overwash fans, cameras were placed as close as possible to the actual location identified from a map, and were not influenced by trails, flood risk, or public exposure.

While our low detection rates illustrated the cryptic nature of red foxes in this study system, we found that red foxes occupied all habitat types, and were not sensitive to the occurrence of other mesopredators (raccoon), large ungulates (feral horses, white-tailed and sika deer), or humans. Interestingly, red foxes on the North End showed no occupancy response to intensive eradication efforts, as occupancy in grid A (and all grids) did not change from one season to the next, despite two consecutive rounds of lethal red fox control conducted in all years of this study between the winter and spring seasons. Specifically, USDA Wildlife Services trapped 9 fox removed in 2012 and 13 fox in 2013 with similar trapping effort (USDA APHIS 2014), yet we found no change in fox occupancy in response to this lethal removal. This lack of response suggests that compensatory immigration or reproduction may be occurring after eradication events. Harding et al. (2001) similarly found that the number of red fox removed in Central California remained relatively constant over 5 years and despite increased removal efforts over this period. Baker and Harris (2006) found that red fox population levels in Great

Britain increase as culling efforts increased, illustrating that losses of red fox in a predator management area were compensated for by new individuals that moved in from a source population. Greentree et al. (2000) found that poison baiting red foxes up to three times a year in Australia had no effect on lamb predation rates or red fox abundance compared to no poison baiting. Newsome et al. (2014) found that even an intensive removal effort (47 red foxes in 12 days) in Australia only reduced the density of foxes from 4.18 to 3.26 per square kilometer. Finally, Towerton et al. (2011) found no effect of red fox control on prey species in Australia, and found that foxes occupied new previously unoccupied sites following implementation of control measures. Thus, there is consistent evidence that predator control is not having the desired effect of reducing fox occupancy or density at a study site.

Food sources on the other hand appear to be an important driver of red fox occupancy in our study area, as illustrated by the strong positive relationship between red fox occupancy and eastern cottontail trap success we found in this study. Baker and Harris (2006) also found that food availability affected red fox density, with lower densities when food was not as abundant. Rabbit sign (burrows and pellets) was often encountered on ASIS in all habitats except for overwash, and red fox photographs were occasionally captured stalking rabbits or with rabbit parts/whole rabbits in their mouths (see Appendix S8). A previous study conducted on red fox diet and denning behavior at Assateague Island also concluded that eastern cottontail was probably one of the most common food items in the red fox diet (Krim et al. 1990). However, none of our habitat variables affected eastern cottontail occupancy or detection. Further research is needed to determine whether microhabitat level factors, such as vegetation density or percent cover, affected eastern cottontail occupancy or detection.

Overall, our findings illustrate two important points related to predator management designed to protect threatened and endangered shorebirds. First, lethal control methods, if intended to reduce red fox populations or presence in proximity to nesting areas, did not have any effect on fox occupancy rates at ASIS and other studies have found similar compensatory responses by red fox to lethal control. Second, we found that red fox occur in all habitats across the barrier island, and are resilient to disturbance posed by humans and hunting pressure. With these points in mind, red fox may be difficult to eradicate in areas where sensitive shorebird species may be negatively affected by their predation effects and thus the effectiveness of other control methods such as nest exclosures should be re-evaluated regularly to ensure they are not negatively affecting shorebird productivity. This study provides an important stepping stone for further research on mammalian shorebird predator population dynamics and habitat use in coastal landscapes. Future research should particularly focus on red fox recolonization and reproduction rates and patterns following removal in coastal habitats, habitat use and movement within shorebird nesting areas, and key food sources for red fox in coastal landscapes, particularly during the shorebird nesting season.

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Tables

Table 1. Top ranking (model likelihood ≥ 0.125) landscape occupancy models and the estimate of occupancy (Ψ) and detection (p) for red fox (*Vulpes vulpes*) and Eastern cottontails (*Sylvilagus floridanus*) across three photographic sampling grids on Assateague Island. Photographic surveys were conducted from 20012-2014 and were combined across all three grids.

Species	Model[a]	AIC	Delta AIC	AIC weight	Model likelihood	K[b]	Psi, Ψ (SE)[c]	p (SE)[d]
Red fox	Ψ (E.cottontailTS),p(macrohabitat)	1892.03	0	0.92	1	4	0.43 (±0.04)	0.26 (±0.02)
E. cottontail	Ψ(grid),p(camera station)	2669.92	0	0.99	1	14	0.56 (±0.03)	0.56 (±0.06)

[a] Ψ = occupancy, p = detection, E.cottontail TS = Eastern cottontail (*Sylvilagus floridanus*) trap success, grid = camera grid A, B, C. See Appendices S6 and S7 for full model set for each species.

[b] K = number of model parameters

[c] Ψ (SE) = occupancy ± standard error

[d] p (SE) = detection ± standard error

Figures

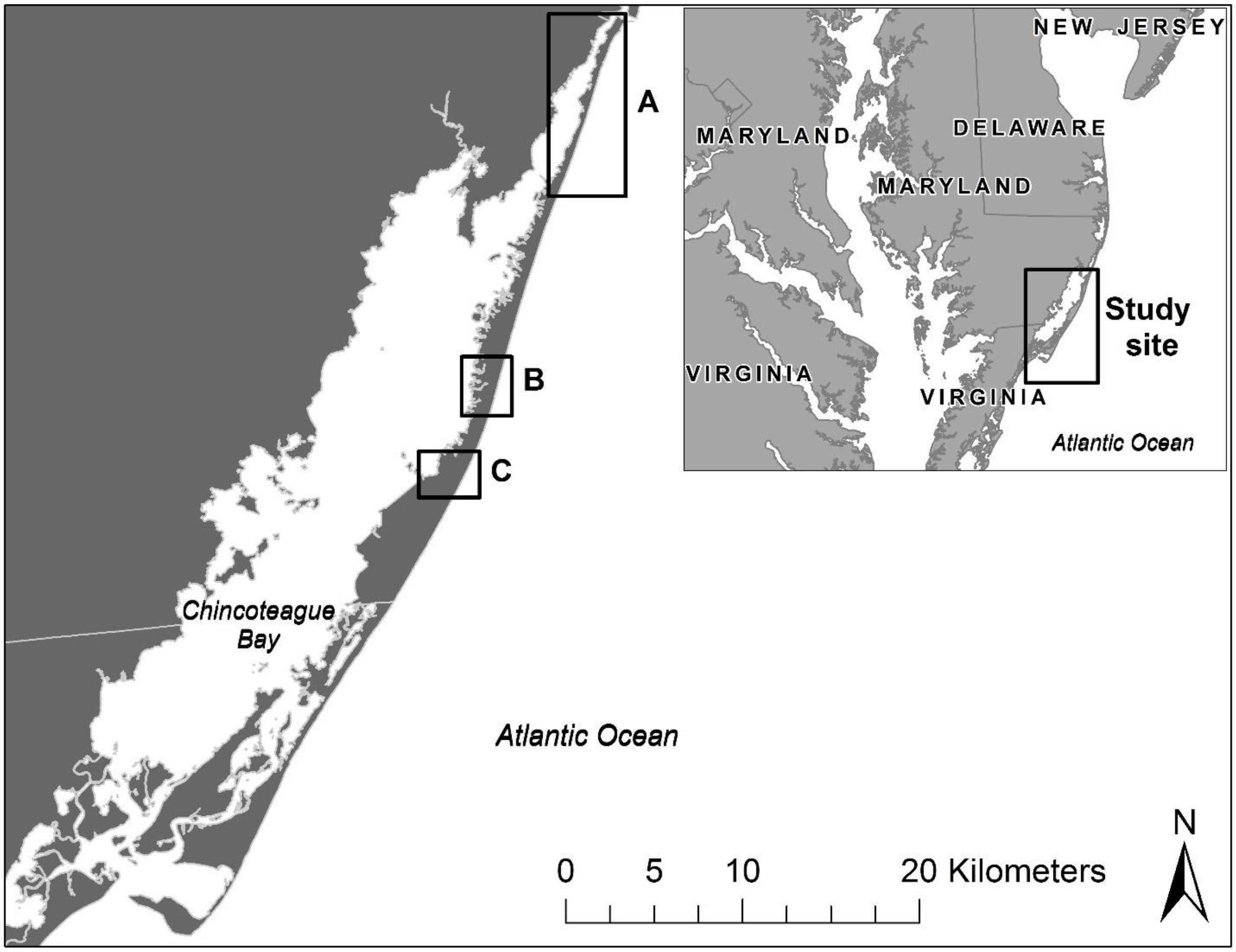


Figure 1. Cameras were set up in three grids at Assateague Island, MD in 2012-2014. Grid A had 36 cameras, and grids B and C each had 25 cameras. All cameras were spaced approximately 300 m apart. See Appendix I for UTM locations of all cameras.

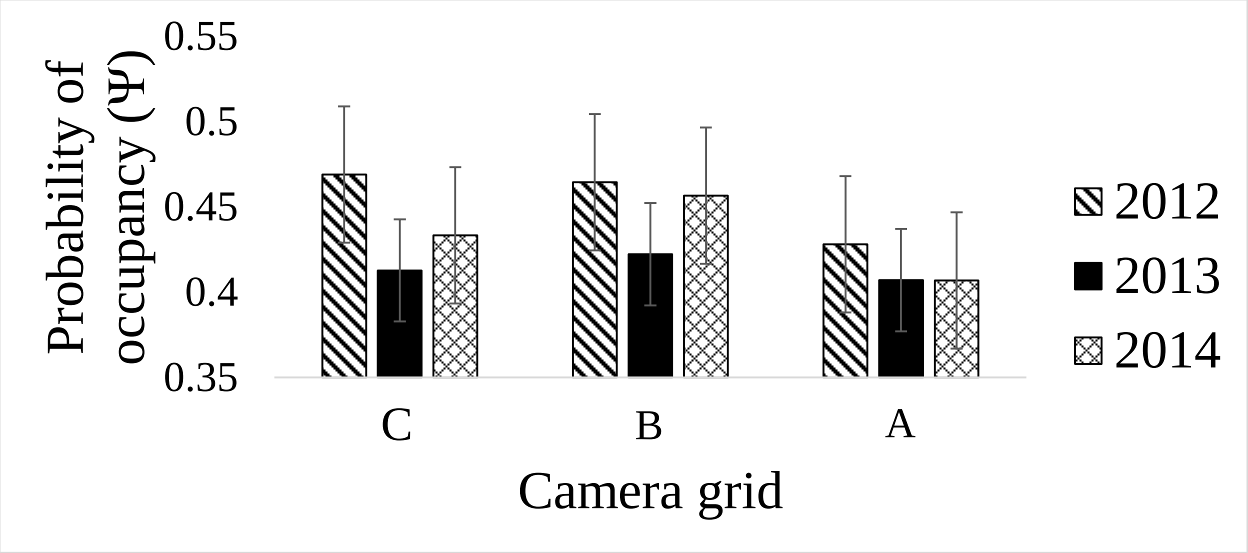


Figure 2. Probability of occupancy (Ψ) for red fox (*Vulpes vulpes*) by year resulting from landscape level occupancy models across three photographic sampling grids on Assateague Island National Seashore, MD from 2012-2014.

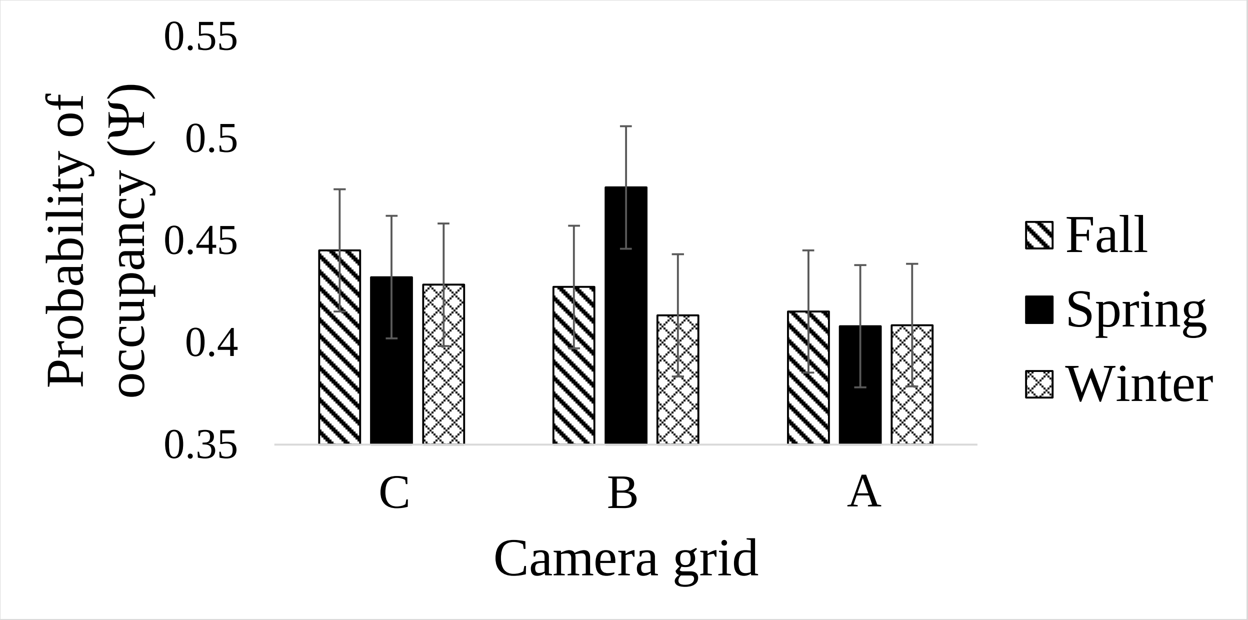


Figure 3. Probability of occupancy (Ψ) for red fox (*Vulpes vulpes*) in three seasons resulting from landscape level occupancy models across three photographic sampling grids on Assateague Island National Seashore, MD from 2012-2014.

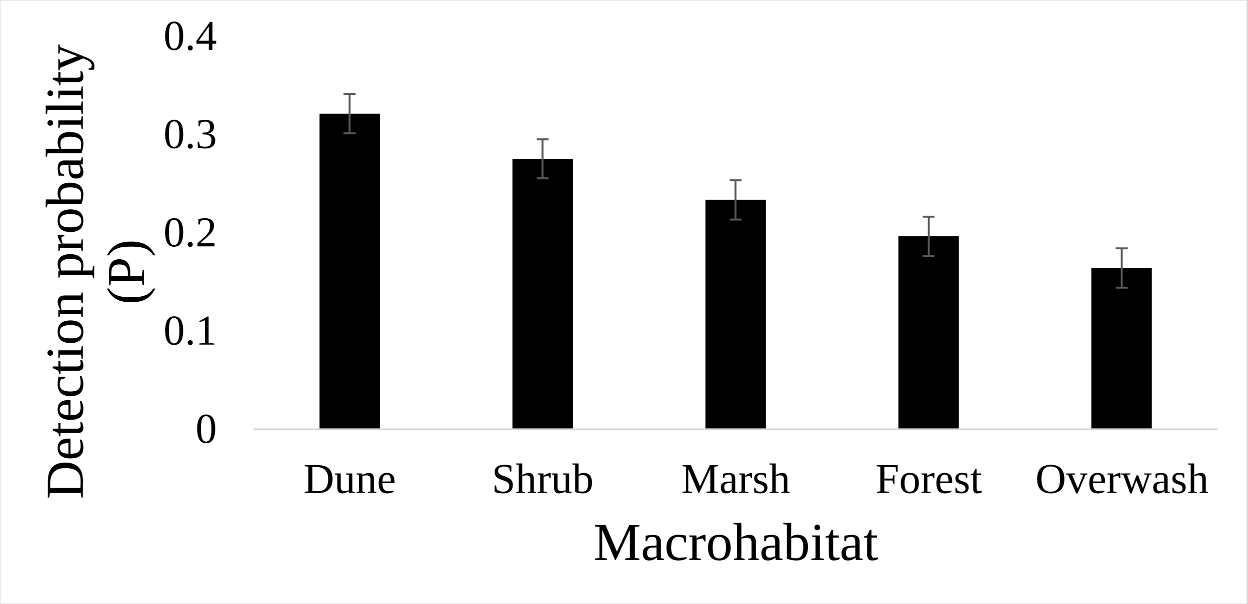


Figure 4. Detection probability (P) for red fox (*Vulpes vulpes*) in five different habitats across three photographic sampling grids on Assateague Island National Seashore, MD from 2012-2014.

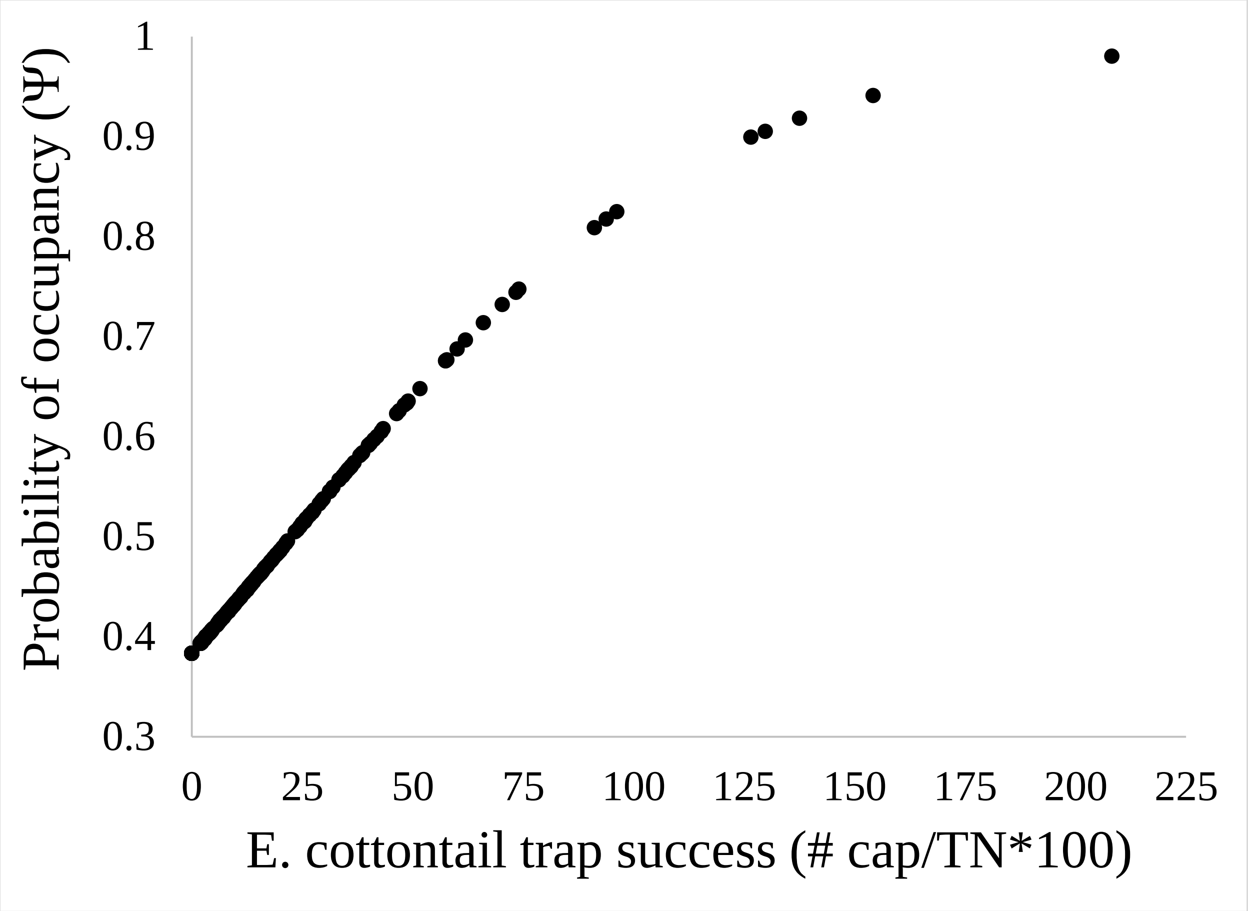


Figure 5. Probability of occupancy (Ψ) for red fox (*Vulpes vulpes*) as a function of eastern cottontail (*Sylvilagus floridanus*) trap success (number of captures/trap night *100) based on regression coefficients (β) resulting from landscape level occupancy models across three photographic sampling grids on Assateague Island National Seashore, MD from 2012-2014.

Appendices

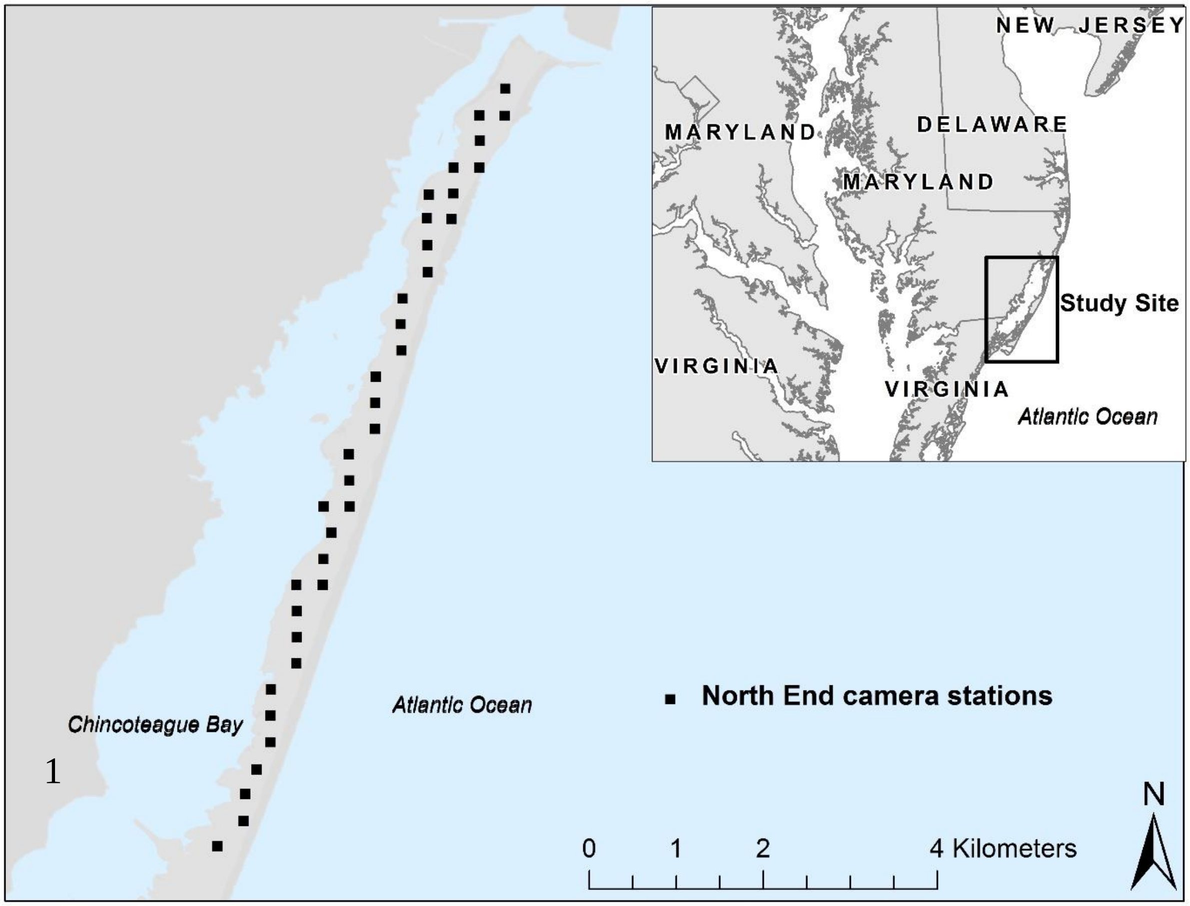
S1. UTM locations of camera trap stations set up in three grids (A, B, C) at Assateague Island National Seashore, MD from 2012-2014.

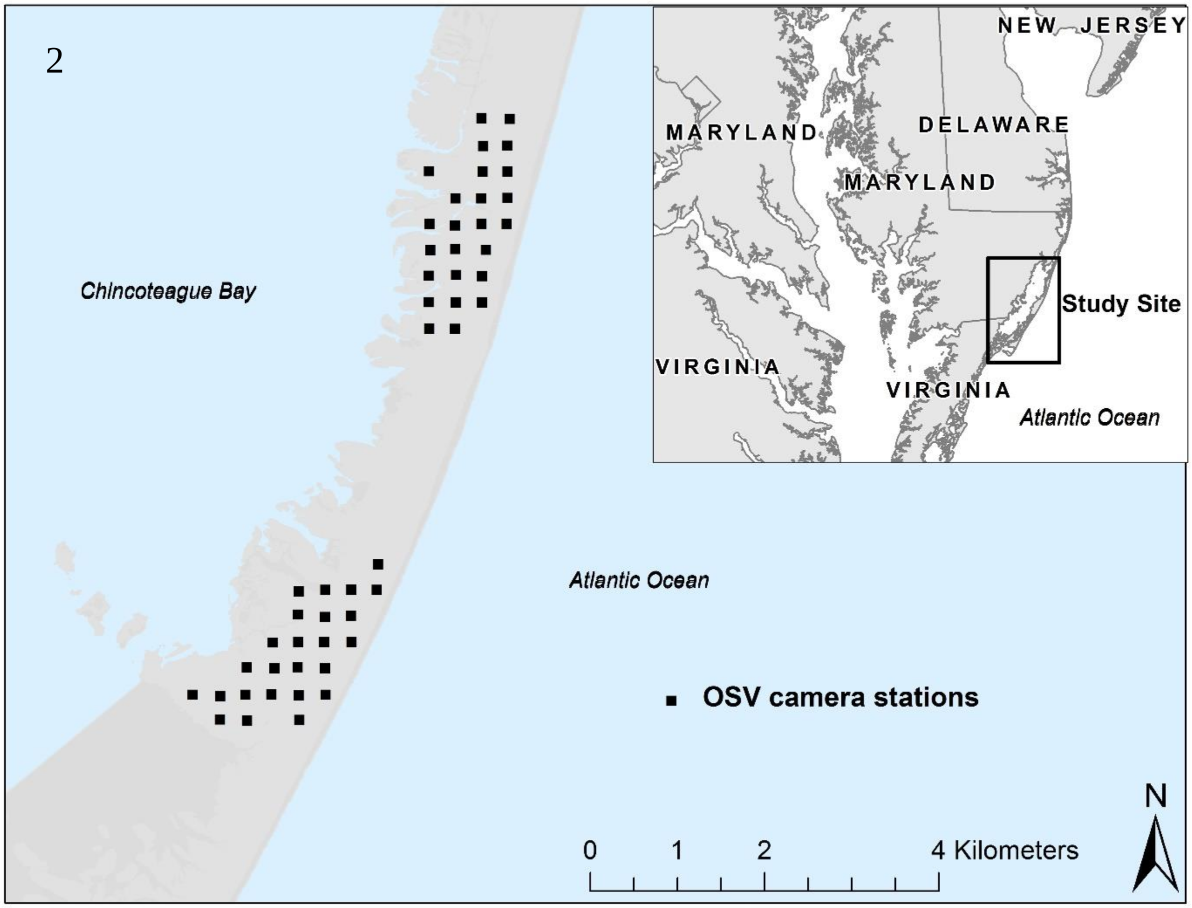
Camera grid	Camera station	NAD 83, Zone 18 N UTM X	UTM Y	Habitat type[a]
A	1	491349	4241354	Deciduous Shrub
A	2	491342	4241043	Dune
A	3	491049	4241048	Deciduous Shrub
A	4	491056	4240757	Dune
A	5	491050	4240450	Marsh
A	6	490753	4240448	Deciduous Shrub
A	7	490752	4240149	Dune
A	8	490467	4240137	Marsh
A	9	490446	4239869	Deciduous Shrub
A	10	490729	4239858	Overwash
A	11	490452	4239554	Dune
A	12	490457	4239246	Dune
A	13	490165	4238942	Deciduous Shrub
A	14	490145	4238649	Dune
A	15	490154	4238348	Overwash
A	16	489858	4238043	Deciduous Shrub
A	17	489852	4237740	Dune
A	18	489849	4237444	Dune
A	19	489547	4237150	Deciduous Shrub
A	20	489555	4236848	Deciduous Shrub
A	21	489556	4236550	Overwash
A	22	489258	4236553	Deciduous Shrub
A	23	489347	4236249	Dune
A	24	489256	4235946	Overwash
A	25	489249	4235651	Overwash
A	26	488943	4235653	Deciduous Shrub
A	27	488950	4235350	Deciduous Shrub
A	28	488951	4235049	Overwash
A	29	488943	4234749	Overwash
A	30	488652	4234447	Deciduous Shrub
A	31	488646	4234148	Deciduous Shrub
A	32	488646	4233843	Dune
A	33	488487	4233526	Dune

A	34	488358	4233247	Dune
A	35	488338	4232935	Dune
A	36	488037	4232648	Deciduous Shrub
B	1	484149	4222160	Pine forest
B	2	484472	4222154	Marsh
B	3	484443	4221846	Deciduous Shrub
B	4	484166	4221842	Deciduous Shrub
B	5	483543	4221554	Pine forest
B	6	484160	4221550	Deciduous Shrub
B	7	484446	4221551	Pine forest
B	8	484447	4221247	Dune
B	9	484145	4221242	Deciduous Shrub
B	10	483850	4221242	Deciduous Shrub
B	11	483550	4220950	Pine forest
B	12	483844	4220931	Marsh
B	13	484148	4220949	Pine forest
B	14	484438	4220947	Dune
B	15	484197	4220652	Deciduous Shrub
B	16	483847	4220662	Deciduous Shrub
B	17	483560	4220650	Pine forest
B	18	483542	4220354	Deciduous Shrub
B	19	483855	4220362	Deciduous Shrub
B	20	484154	4220350	Dune
B	21	484154	4220047	Dune
B	22	483852	4220048	Pine forest
B	23	483541	4220052	Pine forest
B	24	483547	4219748	Pine forest
B	25	483844	4219745	Deciduous Shrub
C	1	482959	4217044	Dune
C	2	482945	4216751	Dune
C	3	482651	4216752	Deciduous Shrub
C	4	482353	4216750	Marsh
C	5	482049	4216733	Marsh
C	6	482041	4216466	Pine forest
C	7	482351	4216439	Pine forest
C	8	482650	4216455	Deciduous Shrub
C	9	482655	4216151	Dune
C	10	482342	4216150	Deciduous Shrub
C	11	482043	4216151	Pine forest
C	12	481750	4216146	Marsh
C	13	481451	4215862	Deciduous Shrub
C	14	481769	4215851	Marsh
C	15	482035	4215864	Pine forest

C	16	482351	4215850	Pine forest
C	17	482357	4215547	Dune
C	18	482048	4215541	Deciduous Shrub
C	19	481736	4215552	Marsh
C	20	481437	4215547	Marsh
C	21	481146	4215529	Pine forest
C	22	480830	4215548	Marsh
C	23	481145	4215265	Deciduous Shrub
C	24	481454	4215250	Deciduous Shrub
C	25	482056	4215259	Pine forest

[a] Habitat type included bayside tidal marshes and mudflats (Marsh), interior pine dominated coniferous (Pine forest), deciduous shrub, and ocean-fronting dunes (Dune) and sandy beaches that include overwash fans (Overwash; open flat low elevation areas resulting from water overwashing during severe storms and high tide events).


NEW JERSEY
MARYLAND
DELAWARE
MARYLAND
Study Site
VIRGINIA
VIRGINIA
Atlantic Ocean
Chincoteague Bay
Atlantic Ocean
■ North End camera stations
1
N
0
1
2
4 Kilometers



S2. Locations of camera trap stations set up in three grids (A, B, C) at Assateague Island National Seashore (ASIS), MD from 2012-2014. Plate 1 shows grid A on the northern tip of the island known as the North End, Plate 2 shows grids B and C in the over sand vehicle (OSV) driving zone at ASIS.

S3. Dates that camera trap stations were operational in three grids (A, B, C) at Assateague Island National Seashore, MD from 2012-2014.

Year	Season	Grid A	Grid B	Grid C
2012	Spring	-	5/2-6/22	4/30-6/15
	Fall	9/27-10/27	8/9-9/28	8/8-9/26
2013	Winter	1/7-2/12	2/13-3/30	2/14-3/30
	Spring	4/19-5/23	5/22-7/10	5/23-7/10
	Fall	9/23-10/27	8/8-9/22	8/9-9/30
2014	Winter	1/10-2/12	2/14-4/2	2/14-3/31
	Spring	4/22-5/25	5/26-7/12	5/26-7/14

S4. Number of camera stations, trap nights, and trap success (TS) for species captured across three photographic sampling grids on Assateague Island from 2012-2014. A total of 11 mammal species were identified from photographs, 5 are not included here because of very low trap success.

Sampling grid	**A**	**B**	**C**
Number of camera stations	36	25	25
Trap nights	6828	7927	7873
Eastern cottontail TS (*Sylvilagus floridanus*)[a]	5.4	12.93	10.21
Feral horse TS (*Equus ferus caballus*)	8.36	7.49	1.71
Human TS	4.14	1.14	0.05
Raccoon TS (*Procyon lotor*)	3.78	15.38	5.65
Sika deer TS (*Cervus nippon*)	8.04	6.4	3.9
White-tailed deer TS (*Odocoileus virginianus*)	0.37	2.9	2.57

[a] Habitat type included bayside tidal marshes and mudflats (Marsh), interior pine dominated coniferous (Pine forest), deciduous shrub, and ocean-fronting dunes (Dune) and sandy beaches that include overwash fans (Overwash; open flat low elevation areas resulting from water overwashing during severe storms and high tide events).

[b] Trap success (TS) was used as an index of co-occurring species activity and was calculated by dividing the total number of capture events of each species by the number of trap nights at each camera station multiplied by 100.

S5. Image showing Reconyx PC90 professional covert infrared cameras (Reconyx, Inc., Holmen, Wisconsin, USA) placed in a wooden box approximately 20 cm above the ground and attached to a metal pole sunk into the sand.

S6. List of all landscape occupancy models for red fox (*Vulpes vulpes*) across three photographic sampling grids on Assateague Island. Photographic surveys were conducted from 2012-2014 and were combined across all three grids.

Model[a]	AIC	Delta AIC	AIC weight	Model likelihood	# Par.[b]
psi(E.cottontailTS),p(macrohabitat)	1892.03	0.00	0.92	1.00	4
psi(.),p(macrohabitat)	1900.38	8.35	0.01	0.02	3
2 groups, Constant P	1901.04	9.01	0.01	0.01	4
psi(whitetailTS),p(macrohabitat)	1902.03	10.00	0.01	0.01	4
psi(macrohabitat),p(macrohabitat)	1902.05	10.02	0.01	0.01	4
psi(raccoonTS),p(macrohabitat)	1902.08	10.05	0.01	0.01	4
psi(distROAD),p(macrohabitat)	1902.10	10.07	0.01	0.01	4
psi(horseTS),p(macrohabitat)	1902.16	10.13	0.01	0.01	4
psi(sikaTS),p(macrohabitat)	1902.24	10.21	0.01	0.01	4
psi(year),p(macrohabitat)	1902.28	10.25	0.01	0.01	4
psi(humanTS),p(macrohabitat)	1902.37	10.34	0.01	0.01	4
psi(season),p(macrohabitat)	1902.38	10.35	0.01	0.01	4
psi(grid),p(macrohabitat)	1902.38	10.35	0.01	0.01	4
2 groups, Survey-specific P	1904.79	12.76	0.00	0.00	14
psi(.),p(E.cottontailTS)	1907.29	15.26	0.00	0.00	3
1 group, Survey-specific P	1912.45	20.42	0.00	0.00	7
psi(.),p(year)	1912.52	20.49	0.00	0.00	3
psi(.),p(distROAD)	1913.58	21.55	0.00	0.00	3
psi(.),p(humanTS)	1914.12	22.09	0.00	0.00	3
psi(.),p(whitetailTS)	1914.93	22.90	0.00	0.00	3
1 group, Constant P	1915.14	23.11	0.00	0.00	2
psi(.),p(raccoonTS)	1916.28	24.25	0.00	0.00	3
psi(.),p(sikaTS)	1916.90	24.87	0.00	0.00	3
psi(.),p(grid)	1917.14	25.11	0.00	0.00	3
psi(.),p(horseTS)	1917.14	25.11	0.00	0.00	3
psi(.),p(season)	1917.14	25.11	0.00	0.00	3

[a] psi = occupancy, p = detection, TS = trap success, E.cottontail = eastern cottontail (*Sylvilagus floridanus*), whitetail = whitetailed deer (*Odocoileus virginianus*), raccoon = raccoon (*Procyon lotor*), horse = feral horse (*Equus ferus caballus*), sika = sika deer (*Cervus nippon*), distROAD = straight line distance of camera from paved road, year = 2012, 2013, 2014, season = spring (April to June), fall (August to October), and winter (January to March), grid = camera grid A on

the northern portion of Assateague Island, MD, and camera grids B, C in the over-sand vehicle zone at Assateague Island National Seashore, MD, macrohabitat = habitat type included bayside tidal marshes and mudflats (Marsh), interior pine dominated coniferous (Pine forest), deciduous shrub, and ocean-fronting dunes (Dune) and sandy beaches that include overwash fans (Overwash; open flat low elevation areas resulting from water overwashing during severe storms and high tide events).

[b] # Par. = number of model parameters

S7. List of all landscape occupancy models for eastern cottontail (*Silvilagus floridanus*) across three photographic sampling grids on Assateague Island. Photographic surveys were conducted from 20012-2014 and were combined across all three grids.

Model[a]	AIC	Delta AIC	AIC weight	Model likelihood	# Par.[b]
2 groups, Survey-specific P	2669.92	0.00	1	1	14
2 groups, Constant P	2683.11	13.19	0	0	4
psi(raccoonTS),p(redfoxTS)	2694.98	25.06	0	0	4
psi(sikaTS),p(redfoxTS)	2695.32	25.40	0	0	4
psi(humanTS),p(redfoxTS)	2716.34	46.42	0	0	4
psi(macrohabitat),p(redfoxTS)	2721.15	51.23	0	0	4
psi(redfoxTS),p(redfoxTS)	2724.86	54.94	0	0	4
psi(distROAD),p(redfoxTS)	2727.88	57.96	0	0	4
psi(year),p(redfoxTS)	2729.11	59.19	0	0	4
psi(.),p(redfoxTS)	2730.92	61.00	0	0	3
psi(whitetailTS),p(redfoxTS)	2732.70	62.78	0	0	4
psi(horseTS),p(redfoxTS)	2732.82	62.90	0	0	4
psi(grid),p(redfoxTS)	2732.92	63.00	0	0	4
psi(season),p(redfoxTS)	2732.92	63.00	0	0	4
psi(.),p(macrohabitat)	2740.89	70.97	0	0	3
psi(.),p(raccoonTS)	2759.19	89.27	0	0	3
1 group, Survey-specific P	2764.13	94.21	0	0	7
psi(.),p(distROAD)	2770.01	100.09	0	0	3
psi(.),p(HorseTS)	2772.65	102.73	0	0	3
psi(.),p(HumanTS)	2772.89	102.97	0	0	3
1 group, Constant P	2773.26	103.34	0	0	2
psi(.),p(year)	2774.75	104.83	0	0	3
psi(.),p(sikaTS)	2774.82	104.90	0	0	3
psi(.),p(whitetailedTS)	2775.17	105.25	0	0	3
psi(.),p(season)	2775.26	105.34	0	0	3
psi(.),p(grid)	2775.26	105.34	0	0	3

[a] psi = occupancy, p = detection, TS = trap success, red fox = red fox (*Vulpes vulpes*), whitetail = whitetailed deer (*Odocoileus virginianus*), raccoon = raccoon (*Procyon lotor*), horse = feral horse (*Equus ferus caballus*), sika = sika deer (*Cervus nippon*), distROAD = straight line distance of camera from paved road, year = 2012, 2013, 2014, season = spring (April to June), fall (August to October), and winter (January to March), grid = camera grid A on the northern

portion of Assateague Island, MD, and camera grids B, C in the over-sand vehicle zone at Assateague Island National Seashore, MD, macrohabitat = habitat type included bayside tidal marshes and mudflats (Marsh), interior pine dominated coniferous (Pine forest), deciduous shrub, and ocean-fronting dunes (Dune) and sandy beaches that include overwash fans (Overwash; open flat low elevation areas resulting from water overwashing during severe storms and high tide events).

[b] # Par. = number of model parameters


2012-06-15 08:19:58 M 1/5 72°F
WIPL 70
RECONYX


2014-06-24 11:42:36 PM M 1/5 73°F
RECONYX

3


2012-05-19 8:45:24 PM M 1/5
63°F
TURTLECAM2
RECONYX

4


2013-10-24 18:38:04 M 5/5
47°F
PC90 COVERT PRO
RECONYX

S8. Images showing red foxes (*Vulpes vulpes*) with rabbit parts and whole rabbits in their mouths (Plates 1-3) and stalking (eyes visible in center of photo) a rabbit (rabbit ears are visible in bottom left corner; Plates 4-5) at camera grid A on Assateague Island National Seashore in October 2013.

CHAPTER 5

RED FOX (*VULPES VULPES*) MOVEMENT ON ASSATEAGUE ISLAND NATIONAL SEASHORE, MARYLAND

Abstract

Mammalian predators have become a key issue in shorebird conservation and management because of concerns of the impact of predation on shorebird breeding success. On the U.S. Atlantic Coast, high rates of human development have coincided with expansions in the ranges of mesopredators such as red foxes (*Vulpes vulpes*), raccoons (*Procyon lotor*), striped skunks (*Mephitis mephitis*), and Virginia opossums (*Didelphis virginiana*). Consequently, extensive human and financial resources are allocated to protecting endangered and threatened shorebirds from predators, including a variety of predator control mechanisms such as nest exclosures and predator removal programs. However, the effectiveness of these mechanisms for control are frequently questioned as we know little about predator ecology in general, and specifically how predator behavior or population parameters respond to such control in coastal systems in particular. We used camera surveys from 2012–2014 to identify individual red foxes (*Vulpes vulpes*), a key shorebird predator, on Assateague Island National Seashore (ASIS), MD, and compared movement patters and ranges for males and females in different seasons and locations in order to better inform predator management actions. We found no significant difference in ranges among individual males and females, nor seasons where individual foxes moved. We detected no movement between camera stations by individuals in fall of all years surveyed (i.e. range of movement was 0 m) and found the largest range of movement (0–6,752.4 m) following red fox removal efforts in the winter seasons of 2013 and 2014 on the North End of ASIS. Our

findings suggest that red foxes on ASIS maintain fairly stable territories but may move large distances to occupy new territory following efforts to eradicate them.

Introduction

Effective mammalian predator management has become a persistent challenge in shorebird conservation as managers seek to minimize losses to predators to maximize nest and chick survival and facilitate population recoveries (USFWS 1996, Schulte et al. 2007). Signs of generalist mammalian predator species, such as red fox (*Vulpes vulpes*), raccoon (*Procyon lotor*), and striped skunk (*Mephitis mephitis*), are commonly encountered in conjunction with failed shorebird nests (Forster 1975, Minsky 1980, MacIvor et al. 1990, Melvin et al. 1992, Loegering and Fraser 1995, Ivan and Murphy 2005, NPS 1991-2014), and these predators are suspected to have major effects on shorebird productivity (Hecht et al. 1999, Kruse et al. 2001). A handful of studies using cameras to monitor shorebird nests have also definitively identified generalist predators, namely raccoon and Virginia opossums (*Didelphis virginiana*), to be the most common known cause of nest failure for Wilson's plovers (*Charadrius wilsonia*), least terns (*Sternula antillarum*), and other colonial nesting waterbirds in North Carolina (Ray 2011, Hillman 2012); however, in many cases the predation by mammalian predators is circumstantial (e.g., tracks around failed nest, Evans 2004). For example, Cohen et al. (2009) showed that reproductive output of the federally-threatened piping plover (*Charadrius melodus*) in West Hampton Dunes was improved when red foxes and cats (*Felis catus*) were removed.

Human development, urbanization, and changes in land use are thought to provide more access and increased food availability for mammalian predators, thus increasing their populations from historical levels (Evans 2004, Scott et al. 2014). This phenomenon has been notable on the U.S. Atlantic Coast, where structures such as bridges and increased refuse from human recreation enable many mammalian species to persist in areas where they were historically absent or present in low numbers (Lauro and Tanacredi 2002). Consequently, red fox and raccoon have been increasingly noted as posing a major potential threat to shorebird populations along the U.S. Atlantic coast, especially the piping plover given its federally-threatened status, but also other coastal bird species of state or regional concern, such as American oystercatchers (*Haematopus palliatus*) and least terns (USFWS 1985, 1996, Patterson et al. 1991, Erwin et al. 2001, Schulte et al. 2007, Cohen et al. 2009, USFWS 2013).

Given that mammalian predators are known to decrease productivity for a number of shorebird and waterbird species, including the piping plover, these predators are intensively managed in most shorebird breeding habitats (Erwin et al. 2001, Neuman et al. 2004, Ivan and Murphy 2005). A number of predator control techniques are commonly employed, including predator exclosures and electric fences around nests, destruction of active den sites, and lethal removal; however, the effectiveness of these techniques for sustained increase in shorebird productivity, and their effects on predator populations are poorly understood (Mayer and Ryan 1991, Cote and Sutherland 1997, Johnson and Oring 2002, Murphy et al. 2003, Neuman et al. 2004, Cohen et al. 2009).

To further understand how to properly manage mammalian predators for shorebird conservation, predator population ecology on barrier islands need to be better understood. In a concurrent study, we examined the occupancy and habitat use of a known shorebird predator, the red fox (*Vulpes vulpes*), on a barrier island in Maryland (Ch. 3 in this dissertation). The red fox is one of the most studied carnivores in North America (Ables 1975); however, its high plasticity in diet, habitat use, spatial movement, and sociality, combined with a lack of studies in coastal habitats, make it difficult to draw valid conclusions about red fox population ecology on barrier islands. To our knowledge, there are no previous studies that specifically focus on red fox population ecology on barrier islands or in coastal habitat along the U.S. Atlantic Coast. One previous study did estimate red fox occupancy in Cape Cod MA as part of a comparison of techniques to estimate occupancy of mesopredators in general, but did not focus specifically on red fox, nor did it associate red fox occupancy with habitat use or movement patterns (O'Connell et al. 2006). Other studies of red fox in coastal areas have been conducted in Europe, but European coastal habitats in those studies differ from those on the U.S. Atlantic Coast in their mesopredator and prey assemblages, weather patterns, habitat diversity, geomorphology, and the absence of barrier islands (Calisti et al. 1990, Cavallini and Lovari 1994, Dekker et al. 2001, Sarmento et al. 2009). Because of their high behavioural plasticity, it is unlikely that we can draw valid conclusions from these European studies about red fox population ecology on the U.S. Atlantic Coast. Thus, our aim was to further understanding of how red foxes use coastal habitat on the U.S. Atlantic Coast to facilitate best design of predator management practices. We studied the spatial movement patterns among individual red foxes on a barrier island in MD. Specifically, we wanted to examine whether there were seasonal, spatial, or sexual differences in fox movement, using individual red foxes identified using photographic sampling techniques.

Methods

Study site

This study was conducted at Assateague Island National Seashore (ASIS) on the Maryland portion of Assateague Island, a 58-km barrier island off the coasts of Maryland and Virginia, U.S. (Fig. 1). ASIS encompasses a variety of habitats ranging from bayside marsh, to pine dominated forest, deciduous brush, dunes, and ocean side sandy beaches that include overwash areas (i.e., open flat low elevation areas resulting from water overwashing during severe storms and high tide events; Morton et al. 2007). A number of imperiled shorebirds, including piping plovers, American oystercatchers (a species of concern in MD), and least terns (a state-threatened species), nest at ASIS (Schupp et al. 2013) and face depredation threats from red foxes, and to a lesser extent raccoons and Virginia opossums. The majority of piping plover nests at ASIS are on the northern 10 km of the island known as the North End, with a smaller number of nests in the over sand vehicle (OSV) zone south of the North End. ASIS has protected all located piping plover nests with predator exclosures every year since at least 1991. In 2008, an adult red fox on the North End learned to access protected nests by jumping on top of exclosures, caving in the netting on top. This fox behavior was thought to be a large contributor to high nest failure (60%) for that year, as fox tracks were found inside damaged exclosures and around nests that had been destroyed or abandoned. Smaller fox tracks were also seen, indicating that young fox were learning this behavior. Concern for plover nest success spurred ASIS staff to employ USDA APHIS to lethally remove all encountered red fox, and occasionally raccoon, on the North End in 2013 and 2014 between our winter and spring seasons (Chapter 4, ASIS 2011).

Field methods

We deployed camera traps at three grid locations on ASIS; one on the North End (grid A), and two more in the OSV zone (grids B and C; Figure 1, Supplementary Information S1, S2). All these locations had frequent red fox sightings prior to our study (J. Kumer, National Park Service, personal communication) and were in or within a few kilometers of known piping plover nesting areas (ASIS 2011), and thus allowed me to assess red fox movements within and around piping plover nesting sites.

Appropriate camera spacing is an important consideration as it can significantly affect estimations of occupancy and population parameters (Stickel 1954,Tanaka 1980,Wegge et al. 2004,Dillon and Kelly 2007). Cameras should be spaced to maximize capture probability for the study target species. Dillon and Kelly (2007) recommend including at least two camera traps per average home range size. However, red fox home range size is highly variable, ranging from estimates as low as 10 ha to over 5000 ha (Macdonald 1987, Voigt 1987), making an average home range size unreliable. Instead, we used the diameter of the smallest home range size to maximize capture probability for the red fox (see Sarmento et al. 2009 for a similar camera spacing methodology for red fox). Therefore, while we generally placed cameras within each habitat type along well established wildlife trails when present, we maintained a minimum spacing of approximately 300 m (±25 m) between each camera station to best accommodate sampling for our target species, red fox.

Cameras were set up in spring (April to June), fall (August to October), and winter (January to March) from 2012–2014. There were 25 cameras each in the two camera grids in the OSV zone (B and C) that operated for approximately 43 days in each season and year. We did not have enough cameras to set up all three camera grids at once, so we staggered the timing of the grids. Grid A on the North End operated from mid-April to mid-May (spring), from mid-September to mid-October (fall), and from mid-Jan to mid-Feb (winter), and had 36 camera stations that operated for approximately 30 days each season and year. Grid A was not set up until the fall season in 2012, and therefore no data was recorded for this grid in spring 2012 (see Supplementary Information S3 for specific dates).

To maximize the number of sampling stations in each habitat type, each camera station consisted of only one camera (see Supplementary Information S4). We did not have any cameras set up on sandy ocean side beach because of a high flood risk, but cameras were set up in every other habitat type present in the study areas (marsh, pine forest, deciduous shrub, dunes, and overwash). We used Reconyx PC90 professional covert infrared cameras (Reconyx, Inc., Holmen, Wisconsin, USA) placed in a wooden box approximately 20 cm above the ground and attached to a metal pole sunk into the sand (Supplementary Information S5). Each camera operated 24h/day and was checked every 10–14 days to ensure they were functioning properly, and to replace batteries and memory cards as needed. Photographs were organized by the date and time of day recorded on each photograph and catalogued for subsequent data analysis.

Data analyses

We used three independent observers to identify individual red foxes from photographic captures; three observers independently identified individual red foxes based on limb coloration patterns, scars, tail shape and coloration pattern, and unique facial colorations (see Supplementary Information S6, S7 for examples). Each observer was unaware of what characteristics or patterns other observers used to identify individuals. Each observer created encounter histories for each individual in each of the photographic surveys in each season across the three camera grids. We used only individuals that all three observers agreed upon in our analyses.

We quantified individual fox movement using the locations of specific camera stations where each individual was seen. We plotted the locations of each individual's sighting on maps of the study area to quantify patterns of movement for each individual. We then calculated the maximum and minimum distance between two cameras that an individual visited, and the movement rate (consecutive distance between 2 cameras/24h time intervals between visits) for each individual, separated by sex (if known), season, and year (Figure 2, Supplementary

Information S8). We tested for differences between sexes (males and females) and seasons where individual foxes were seen at multiple cameras, and the three camera grids. We used unpaired t-tests to test sex and seasonal differences, or Mann-Whitney tests if the data did not fit the assumptions of normality or homogeneous variances. We used one-way Kruskal-Wallis tests to compare differences among camera grids and conducted statistical analyses in MaxStat Software (Jever, Germany), using an alpha level of 0.05 for all statistical tests. Finally, we also tabulated the camera stations that were visited by more than one individual, comparing the number of individuals and sexes (if known) visiting each camera, and in which season and habitat (marsh, pine forest, deciduous brush, dunes, and overwash) the camera was located.

Results

In total, we identified 41 red fox individuals (see Appendix S6, S7) for examples); no individuals were seen across seasons, years, or grids. We also identified 5 individual kits in spring 2012 but we did not include them in this analysis because we were not able to tell them apart towards the end of the season after they had developed more adult features. The number of individuals identified within each season ranged from a low of 3 in spring 2013 to a high of 10 in spring 2014 (Table1).

The average percent of red fox photographs that were identified to individuals over the entire study period was low (26%) and resight rates for individuals were also low (Table 1). Only 27 of the 41 individuals were resighted and 10 of those 27 were resighted just once. The average number of resights for each season ranged from 0.67 to 4, although this higher resight of 4 was largely due to one individual that was resighted 9 times (average number of resights without this individual was 1.33). Within each grid, a maximum of four individuals were identified and resighted, with a median of two individuals identified and resighted over the entire study period (per grid; Table 2).

Most (28 out of 41) individuals were seen at just one camera, with other individuals being seen at 2–9 different cameras. In spring the average number of cameras visited by each individual was 1.8, and in the winter an average of 2.4 cameras were visited by each individual. More than one individual was seen at the same camera station within the same season on 8 occasions (5 occasions in grid C, 3 occasions in grid B) in all seasons except for fall and in all grids except for grid A. In all these occasions, only two individuals were seen, and consisted of a male and female (for all cases where sex could be discerned for both individuals; Table 3).

All of the red fox individuals identified in the fall seasons were resighted at just one camera, whereas individuals resighted in spring and winter seasons were sometimes resighted at multiple cameras. The largest range of movement for one individual seen between any two cameras was 291.9–6,752.4 m in grid A in spring 2014 (Table 4). Average distance between two cameras where individual foxes were seen did not differ significantly among sexes (Mann-Whitney test; $U(1) = 0.49$, $p = 0.78$; median (range) females = 0 (0–1074.5 m), males = 0 (0–1199.2 m)). There was also no significant difference between seasons where foxes moved among cameras (i.e. spring, winter; Mann-Whitney test; $U(1) = 128$, $p = 0.22$; median(range) spring = 0 (0–2608.1, winter = 320.9 (0–2180.8)). Despite some disproportionately large movements by an individual in grid A that moved a maximum distance of 6,752.4 m, average distances also did not differ significantly among grids (Kruskal-Wallis test; $H(2) = 2.05$, $p = 0.36$; median (range) grid A = 0 (0–2608.13), grid B = 0 (0–1199.18), grid C = 0 (0–1074.46); Table 4).

Discussion

To our knowledge, this is the first study to use cameras to individually identify red fox in a barrier island system and to assess seasonal, spatial, and sexual differences in movement. The lack of any differences in movement between sexes contrasts with other studies that have found smaller home ranges sizes for females (2.12 km^2 (1642 m diameter) versus 3.04 km^2 (1128 m diameter) for males; Rountree 2004) and shorter mean dispersal distances (11 km for females, 31 km for males; Storm et al. 1976). However, sexual differences in red fox movement are varied because other studies have found no significant differences in male and female red fox home range size (Meek and Saunders 2000, Dekker et al. 2001).

Our finding of no seasonal differences in red fox movement between spring and winter seasons contrasts other studies that have found that red fox dispersal is influenced by reproduction and that foxes in reproductive mode move farther (8.57±0.78 km) than foxes not in reproductive mode (4.84±0.52 km; Soulsboury et al. 2011). However, our observation of a lack of detection of foxes across camera stations in the fall seasons is consistent with a general trend for seasonality in movement, with more movement in the spring and winter seasons than in the fall in our study area. Red foxes are territorial, and young red foxes typically leave their natal den to disperse to new habitat in late summer. However, some juveniles do not disperse and stay to help raise subsequent litters and others disperse in late fall as late as October (Jensen 1973, Storm et al. 1976). The lack of detected movement we found for a majority of the individuals in our study, and for all individuals in fall, indicates that our camera spacing probably reflected typical territory sizes individual red foxes in our study system. Furthermore, our finding that the sightings of multiple individuals at a single camera station were all of one male/one is additional support that our camera spacing may have been adequately spaced to capture one territorial pair of foxes per station.

Estimates of actual territory size and density could not be computed from the low sample sizes and recapture rates in this study, and individuals that did move between cameras could have been missed given low resight rates (see Chapter 4). We were unable to identify individuals across seasons or years and could not discern individual movement variation over long time periods. Although we identified 41 individuals overall, we did not have sufficient recaptures in each season to estimate density. Density estimates from samples with very low capture rates are not reliable because they result in high standard error (McCarthy et al. 2009). Low detection in carnivores is a common problem that prevents reliable density estimates when recapture rates are extremely low as in this study (Maffei et al. 2004, Gerber et al. 2011). We were able to estimate occupancy in a previous study and make strong associations between occupancy and habitat factors, but an estimate of density is also desirable for making association to shorebird productivity. Future studies that aim to estimate red fox density should use 2 cameras per station and use bait to attract red foxes. Bait could be placed in a location that would encourage lateral views of red foxes for better identification. Gerber et al. (2011) found no significant difference in density estimates using lures to attract animals to cameras compared to using no lures, so bias introduced by bait or lures is not always expected but should be assessed when possible. Thus, future studies that may use lures could compare capture rates to this study to assess whether there would be any bias.

Overall, the results of this study show that red foxes likely maintain small but stable territories. However, the large movement (6, 752.4 m) by one individual we saw on the North End indicates that red foxes may move into newly opened territories quickly. Our observation of a large movement followed a red fox eradication effort conducted yearly in between our winter and spring seasons at ASIS as part of predator management for shorebird conservation (USDA

APHIS 2014). Removing red fox from an area may thus promote increased movement by other red foxes that move in to occupy vacant territory. This compensatory immigration has been found in other studies of red fox movement. For example, Harding et al. (2001) found that the number of red fox removed remained relatively constant over 5 years despite increased removal efforts over this period. Baker and Harris (2006) found that red fox population levels do not decrease with culling, and further found that they actually increase as culling efforts increased, illustrating that losses of red fox in a predator management area are compensated for by new individuals that move in from a source population outside of this area. Towerton et al. (2011) also found that foxes occupied new previously unoccupied sites following implementation of control measures. Our finding of increased movement following red fox removal was based on only one individual, but compensatory immigration could have important implications for shorebird conservation. Thus further study should be conducted on red fox movement following removal efforts, particularly in areas with breeding shorebirds.

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Tables

Table 1. Total individuals identified, capture events, and % photos identified of red fox (*Vulpes vulpes*) at 3 camera trap grids (C, B, A) from South to North on Assateague Island National Seashore, MD in spring, fall, and winter seasons from 2012–2014.

Season[a]	Grid	Total individuals	Total Capture events	% photos identified
Spring 2012	C	3	20	25
	B	4	100	15
Fall 2012	C	2	23	26
	B	2	50	14
	A	1	22	5
Winter 2013	C	2	77	19
	B	1	20	15
	A	1	53	4
Spring 2013	C	3	13	31
	B	0	4	0
	A	0	1	0
Fall 2013	C	2	17	41
	B	2	4	50
	A	2	16	13
Winter 2014	C	2	11	27
	B	2	39	28
	A	2	41	12
Spring 2014	C	4	18	56
	B	5	20	55
	A	1	13	77

[a] Spring season was from April to June, fall from August to October, and winter from January to March.

Table 2. Total red fox (*Vulpes vulpes*) individuals and resightings at 3 camera trap grids (C, B, A) from South to North on Assateague Island National Seashore, MD in spring, fall, and winter seasons from 2012–2014.

Season[a]	Grid	Individual[b]	Number of resights[c]
Spring 2012	C	1	1
		2	1
		3	0
	B	4	2
		5	2
		6	7
		7	0
Fall 2012	C	8	3
		9	1
	B	10	1
		11	4
	A	12	0
Winter 2013	C	13	4
		14	9
	B	15	2
	A	16	1
Spring 2013	C	17	0
		18	2
		19	0
Fall 2013	C	20	3
		21	2
	B	22	0
		23	0
	A	24	0
		25	0
Winter 2014	C	26	1
		27	0
	B	28	9
		29	0
	A	30	2
		31	1
Spring 2014	C	32	3
		33	3
		34	0

	35	0
B	36	1
	37	0
	38	3
	39	1
	40	1
A	41	9

[a] Spring season was from April to June, fall from August to October, and winter from January to March.

[b] Individuals were numbered sequentially

[c] Resight means the same individual that was captured again on camera

Table 3. Habitat and sex of red fox (*Vulpes vulpes*) individuals that were seen at the same camera station at 2 camera trap grids (C, B) from South to North on Assateague Island National Seashore, MD from in spring and winter seasons from 2012–2014.

Season[a]	Grid	Number of fox individuals seen	Habitat[b]	Sex[c]
Spring 2012	C	2	Marsh	F, M
	B	2	Dune	U, U
		2	Shrub	F, M
Winter 2013	C	2	Shrub	M, U
Spring 2014	C	2	Dune	F, U
		2	Dune	U, M
		2	Shrub	U, U
	B	2	Shrub	F, M

[a] Spring season was from April to June, fall from August to October, and winter from January to March.

[b] Habitat included bayside marsh, dune habitat on the ocean side, and deciduous shrub in the interior

[c] Sex included female (F), male (M), and unidentified sex (U)

Table 4. Maximum, minimum, and average distance (m) between all combinations of cameras where red fox (*Vulpes vulpes*) individuals were sighted at 3 camera trap grid locations on Assateague Island National Seashore, MD in spring, fall, and winter seasons from 2012–2014.

Year	Season[a]	Fox ID	Sex[b]	Grid	Number of cameras visited	Number of resights[c]	Max distance (m) between resight locations	Min distance (m) between resight locations	Average distance (m) between resight locations[d]
2012	Spring	1	U	C	2	1	422	422	421.5
		2	F	C	2	1	434	434	433.9
		3	M	C	1	0	0	0	0
		4	U	B	1	2	0	0	0
		5	U	B	1	2	0	0	0
		6	F	B	1	7	0	0	0
		7	M	B	1	0	0	0	0
	Fall	8	M	C	1	3	0	0	0
		9	F	C	1	1	0	0	0
		10	M	B	1		0	0	0
		11	F	B	1	4	0	0	0
		12	M	A	1	0	0	0	0
2013	Winter	13	M	C	3	4	424	293	337.3
		14	U	C	4	9	1711	601	1056.3
		15	U	B	2	2	305	305	304.5
		16	U	A	1	1	0	0	0
	Spring	17	U	C	1	0	0	0	0
		18	M	C	2	2	293	293	293.3
		19	U	C	1	0	0	0	0
	Fall	20	M	C	1	3	0	0	0
		21	U	C	1	2	0	0	0

		22	U	B	1	0	0	0	0
		23	U	B	1	0	0	0	0
		24	U	A	1	0	0	0	0
		25	U	A	1	0	0	0	0
2014	Winter	26	M	C	2	1	943	943	943.3
		27	U	C	1	0	0	0	0
		28	M	B	7	9	2490	400	1199.2
		29	F	B	1	0	0	0	0
		30	U	A	2	2	2181	2181	2180.8
		31	U	A	1	1	0	0	0
	Spring	32	F	C	2	3	1075	1075	1074.5
		33	U	C	3	3	861	309	614.4
		34	M	C	1	0	0	0	0
		35	U	C	1	0	0	0	0
		36	M	B	2	1	933	933	932.9
		37	U	B	1	0	0	0	0
		38	F	B	1	3	0	0	0
		39	M	B	1	1	0	0	0
		40	U	B	1	1	0	0	0
		41	U	A	9	9	6752	292	2608.1

[a] Spring season was from April to June, fall from August to October, and winter from January to March.

[b] Sex included female (F), male (M), and unidentified sex (U).

[c] Resight means the same individual that was captured again on camera

[d] Average distance (m) between resight locations was calculated as the mean of all distances between any two cameras that an individual fox visited.

Figures

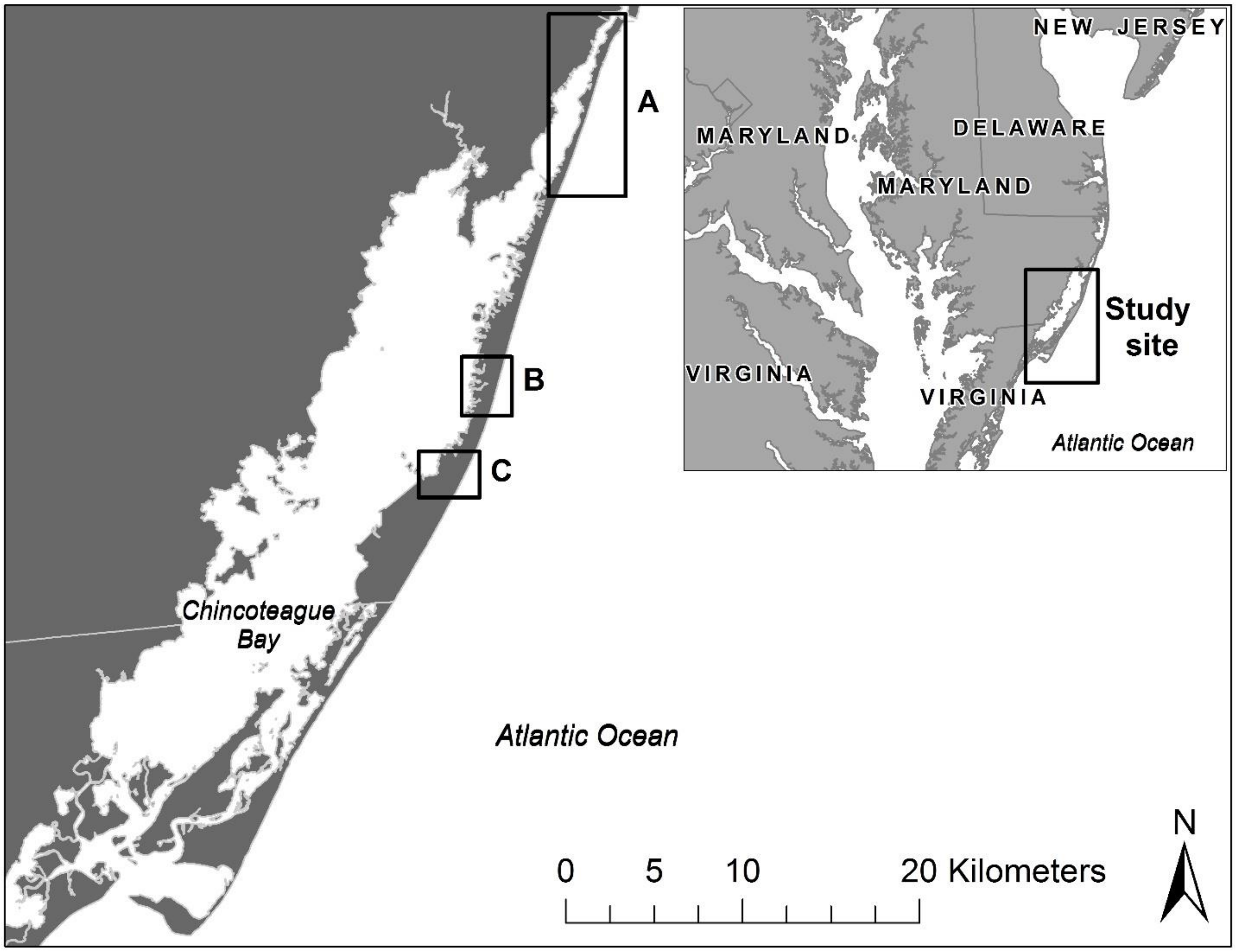


Figure 1. Cameras were set up in three grids at Assateague Island, MD in 2012–2014. Grid A had 36 cameras, and grids B and C each had 25 cameras. All cameras were spaced approximately 300 m apart. See Supplementary Information Table S1 for UTM locations of all cameras.

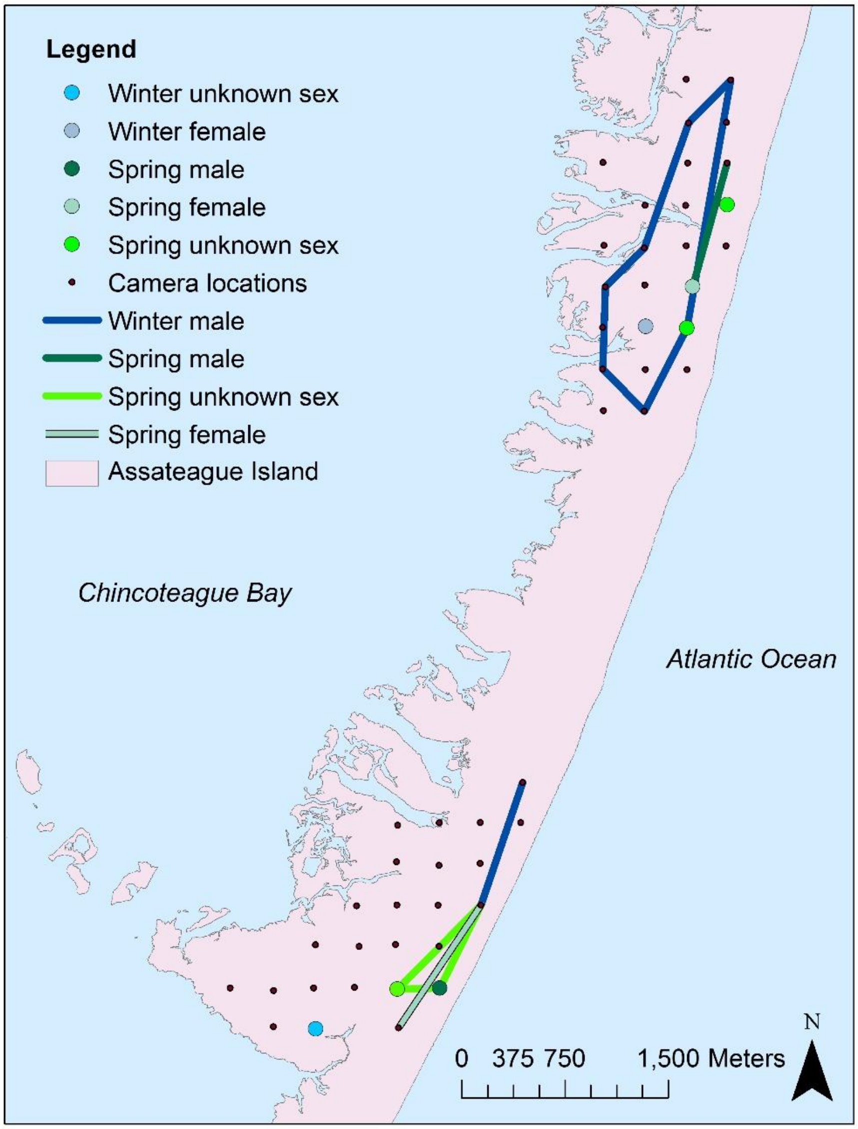


Figure 2. Example map showing camera station locations and individual red fox movements for males, females, and unknown sex in spring and winter at Assateague Island National Seashore, MD in 2014. Movements of red fox individuals at camera grids B (top) and C (bottom) at Assateague Island National Seashore, MD. Continuous lines represent one individual that was seen at multiple camera stations. Dots represent individuals that were only seen at one camera. Maps showing movements for all years (2012–2014) and all camera grid locations (grids A, B, C) are in Appendix S8.

Appendices

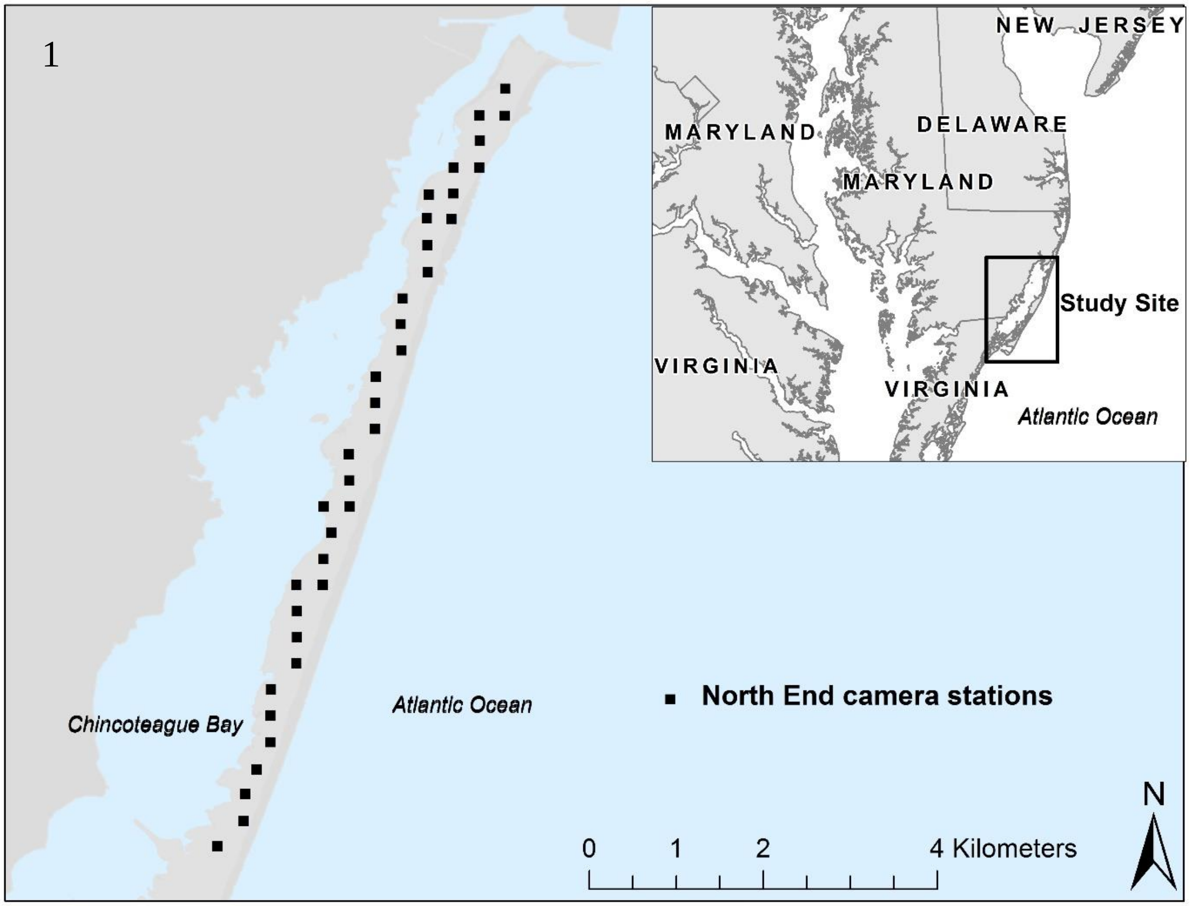
S1. UTM locations of camera trap stations set up in three grids (A, B, C) at Assateague Island National Seashore, MD from 2012-2014.

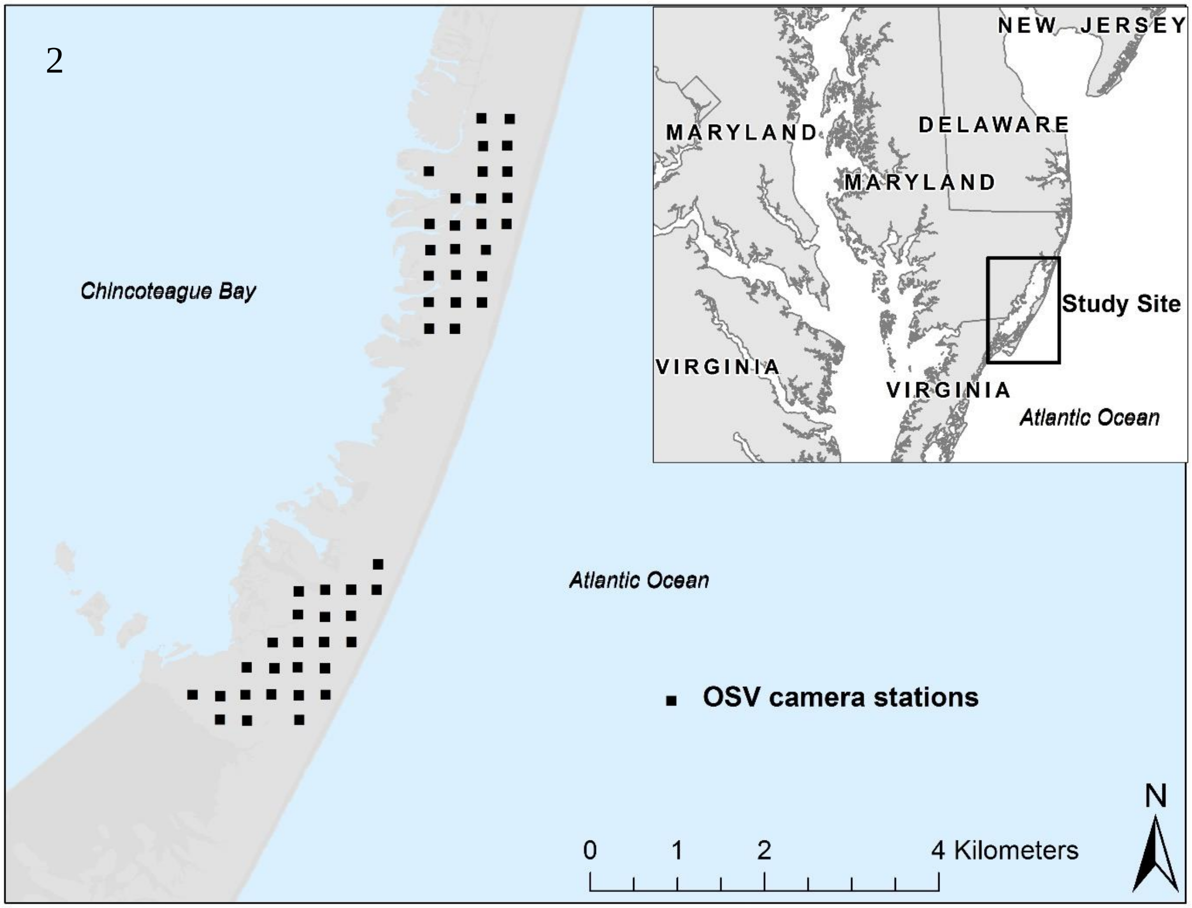
		NAD 83, Zone 18 N		Habitat type[a]
Camera grid	Camera station	UTM X	UTM Y	
A	1	491349	4241354	Deciduous Shrub
A	2	491342	4241043	Dune
A	3	491049	4241048	Deciduous Shrub
A	4	491056	4240757	Dune
A	5	491050	4240450	Marsh
A	6	490753	4240448	Deciduous Shrub
A	7	490752	4240149	Dune
A	8	490467	4240137	Marsh
A	9	490446	4239869	Deciduous Shrub
A	10	490729	4239858	Overwash
A	11	490452	4239554	Dune
A	12	490457	4239246	Dune
A	13	490165	4238942	Deciduous Shrub
A	14	490145	4238649	Dune
A	15	490154	4238348	Overwash
A	16	489858	4238043	Deciduous Shrub
A	17	489852	4237740	Dune
A	18	489849	4237444	Dune
A	19	489547	4237150	Deciduous Shrub
A	20	489555	4236848	Deciduous Shrub
A	21	489556	4236550	Overwash
A	22	489258	4236553	Deciduous Shrub
A	23	489347	4236249	Dune
A	24	489256	4235946	Overwash
A	25	489249	4235651	Overwash
A	26	488943	4235653	Deciduous Shrub
A	27	488950	4235350	Deciduous Shrub
A	28	488951	4235049	Overwash
A	29	488943	4234749	Overwash
A	30	488652	4234447	Deciduous Shrub
A	31	488646	4234148	Deciduous Shrub
A	32	488646	4233843	Dune
A	33	488487	4233526	Dune

A	34	488358	4233247	Dune
A	35	488338	4232935	Dune
A	36	488037	4232648	Deciduous Shrub
B	1	484149	4222160	Pine forest
B	2	484472	4222154	Marsh
B	3	484443	4221846	Deciduous Shrub
B	4	484166	4221842	Deciduous Shrub
B	5	483543	4221554	Pine forest
B	6	484160	4221550	Deciduous Shrub
B	7	484446	4221551	Pine forest
B	8	484447	4221247	Dune
B	9	484145	4221242	Deciduous Shrub
B	10	483850	4221242	Deciduous Shrub
B	11	483550	4220950	Pine forest
B	12	483844	4220931	Marsh
B	13	484148	4220949	Pine forest
B	14	484438	4220947	Dune
B	15	484197	4220652	Deciduous Shrub
B	16	483847	4220662	Deciduous Shrub
B	17	483560	4220650	Pine forest
B	18	483542	4220354	Deciduous Shrub
B	19	483855	4220362	Deciduous Shrub
B	20	484154	4220350	Dune
B	21	484154	4220047	Dune
B	22	483852	4220048	Pine forest
B	23	483541	4220052	Pine forest
B	24	483547	4219748	Pine forest
B	25	483844	4219745	Deciduous Shrub
C	1	482959	4217044	Dune
C	2	482945	4216751	Dune
C	3	482651	4216752	Deciduous Shrub
C	4	482353	4216750	Marsh
C	5	482049	4216733	Marsh
C	6	482041	4216466	Pine forest
C	7	482351	4216439	Pine forest
C	8	482650	4216455	Deciduous Shrub
C	9	482655	4216151	Dune
C	10	482342	4216150	Deciduous Shrub
C	11	482043	4216151	Pine forest
C	12	481750	4216146	Marsh
C	13	481451	4215862	Deciduous Shrub
C	14	481769	4215851	Marsh
C	15	482035	4215864	Pine forest

C	16	482351	4215850	Pine forest
C	17	482357	4215547	Dune
C	18	482048	4215541	Deciduous Shrub
C	19	481736	4215552	Marsh
C	20	481437	4215547	Marsh
C	21	481146	4215529	Pine forest
C	22	480830	4215548	Marsh
C	23	481145	4215265	Deciduous Shrub
C	24	481454	4215250	Deciduous Shrub
C	25	482056	4215259	Pine forest

[a] Habitat type included bayside tidal marshes and mudflats (Marsh), interior pine dominated coniferous (Pine forest), deciduous shrub, and ocean-fronting dunes (Dune) and sandy beaches that include overwash fans (Overwash; open flat low elevation areas resulting from water overwashing during severe storms and high tide events).


1
NEW JERSEY
MARYLAND
DELAWARE
MARYLAND
Study Site
VIRGINIA
VIRGINIA
Atlantic Ocean
Chincoteague Bay
Atlantic Ocean
■ North End camera stations
N
0 1 2 4 Kilometers



S2. Locations of camera trap stations set up in three grids (A, B, C) at Assateague Island National Seashore (ASIS), MD from 2012-2014. Plate 1 shows grid A on the northern tip of the island known as the North End, Plate 2 shows grids B and C in the over sand vehicle (OSV) driving zone at ASIS.

S3. Dates that camera trap stations were operational in three grids (A, B, C) at Assateague Island National Seashore, MD from 2012-2014.

Year	**Season**	**Grid A**	**Grid B**	**Grid C**
2012	Spring	-	5/2-6/22	4/30-6/15
	Fall	9/27-10/27	8/9-9/28	8/8-9/26
2013	Winter	1/7-2/12	2/13-3/30	2/14-3/30
	Spring	4/19-5/23	5/22-7/10	5/23-7/10
	Fall	9/23-10/27	8/8-9/22	8/9-9/30
2014	Winter	1/10-2/12	2/14-4/2	2/14-3/31
	Spring	4/22-5/25	5/26-7/12	5/26-7/14

S4. Number of camera stations (total and by macrohabitat), trap nights, and trap success (TS) for species captured across three photographic sampling grids on Assateague Island from 2012-2014. A total of 11 mammal species were identified from photographs, 5 are not included here because of very low trap success.

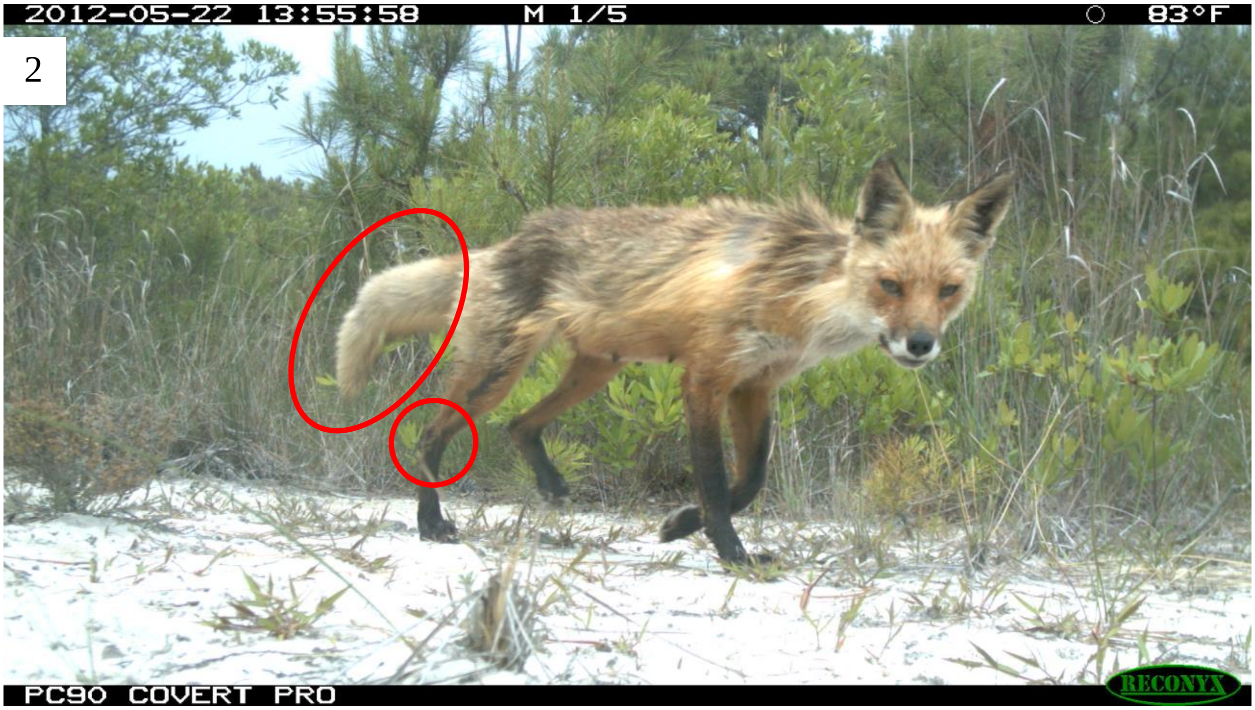
Study site	**A**	**B**	**C**
Total number of camera stations	36	25	25
Number of camera stations by macrohabitat[a]			
Marsh	2	2	7
Pine forest	0	9	7
Deciduous shrub	14	10	7
Dune	13	4	4
Overwash	7	0	0
Trap nights	6828	7927	7873
Eastern cottontail TS (*Sylvilagus floridanus*)[b]	5.40	12.93	10.21
Feral horse TS (*Equus ferus caballus*)	8.36	7.49	1.71
Human TS	4.14	1.14	0.05
Raccoon TS (*Procyon lotor*)	3.78	15.38	5.65
Sika deer TS (*Cervus nippon*)	8.04	6.40	3.90
White-tailed deer TS (*Odocoileus virginianus*)	0.37	2.90	2.57

[a] Habitat type included bayside tidal marshes and mudflats (Marsh), interior pine dominated coniferous (Pine forest), deciduous shrub, and ocean-fronting dunes (Dune) and sandy beaches that include overwash fans (Overwash; open flat low elevation areas resulting from water overwashing during severe storms and high tide events).

[b] Trap success (TS) was used as an index of co-occurring species activity and was calculated by dividing the total number of capture events of each species by the number of trap nights at each camera station multiplied by 100.

S5. Image showing Reconyx PC90 professional covert infrared cameras (Reconyx, Inc., Holmen, Wisconsin, USA) placed in a wooden box approximately 20 cm above the ground and attached to a metal pole sunk into the sand.


1


2

S6. Example of an individual red fox (*Vulpes vulpes*) identified using unique characteristics. This individual was identified by a kinked tail and dark spot on the right hind limb. This individual was captured on May 22, 2012 at 13:03 (Plate 1) and was captured again on the same date at 13:55 at a different camera station (Plate 2). This individual was also identified as a lactating female by the presence of teats visible in Plate 2.

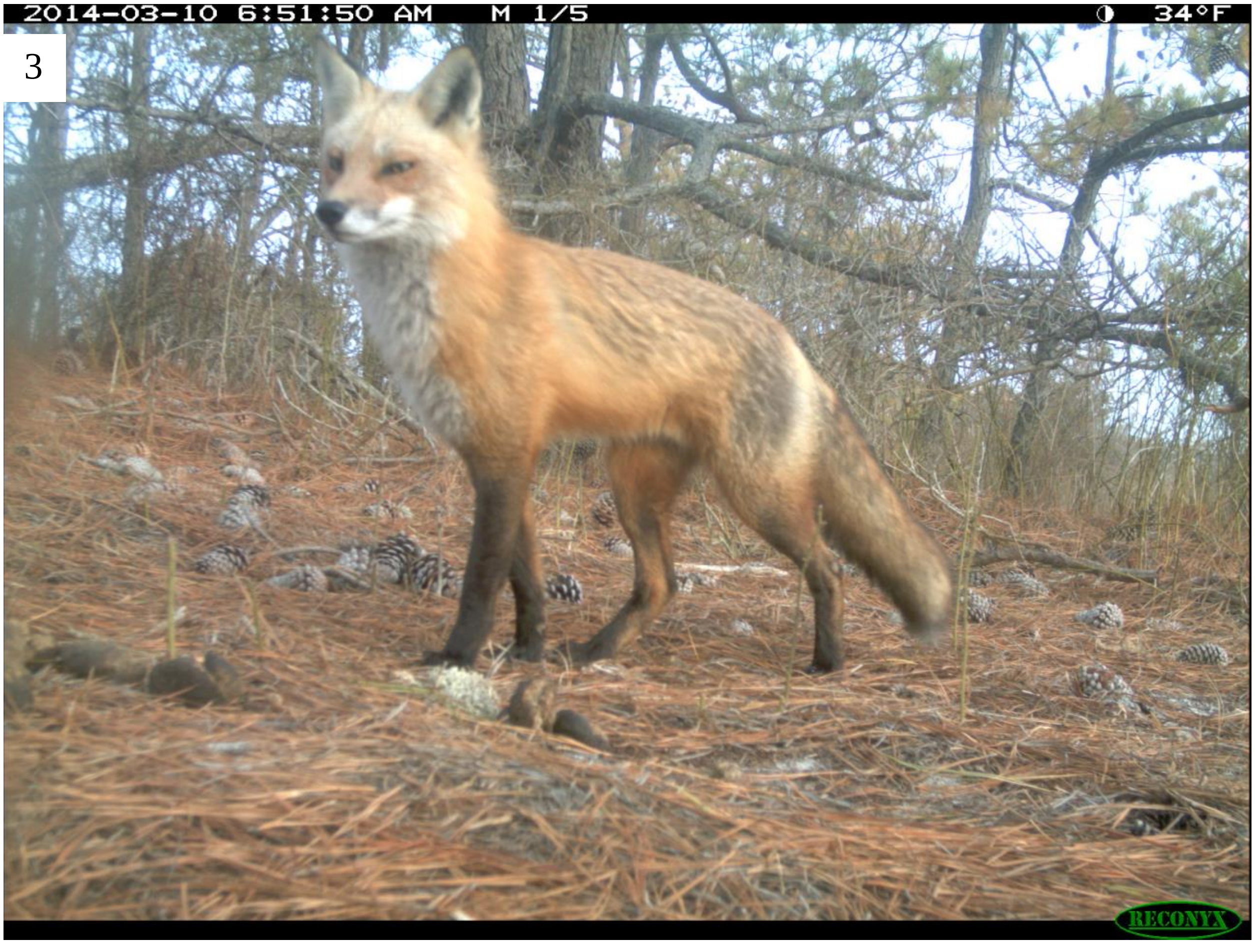

1

2014-03-01 06:35:24
M 1/5
21°F
WIPL 67
RECONYX


2

2014-03-05 16:15:37
M 1/5
45°F
WIPL 67
RECONYX

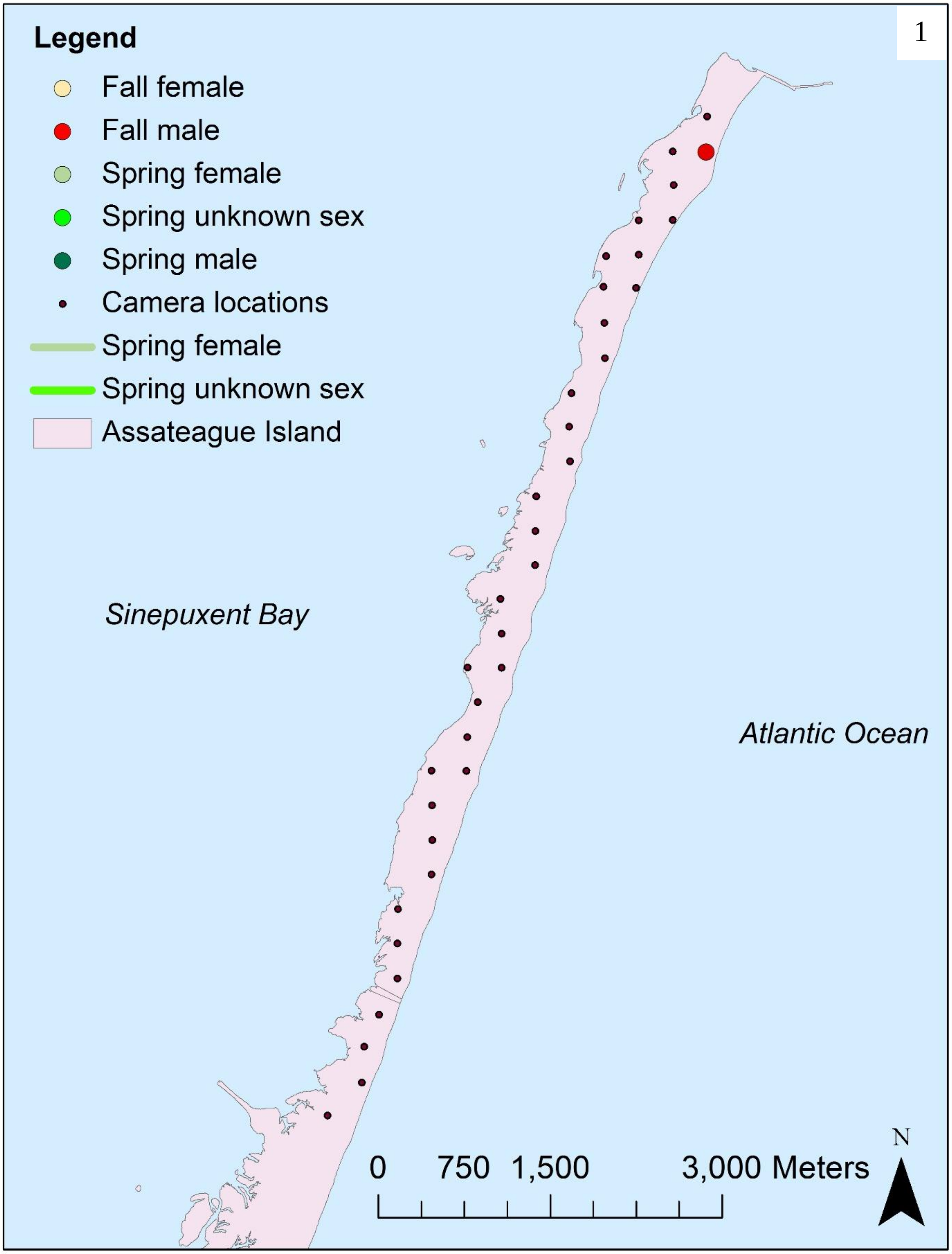
3

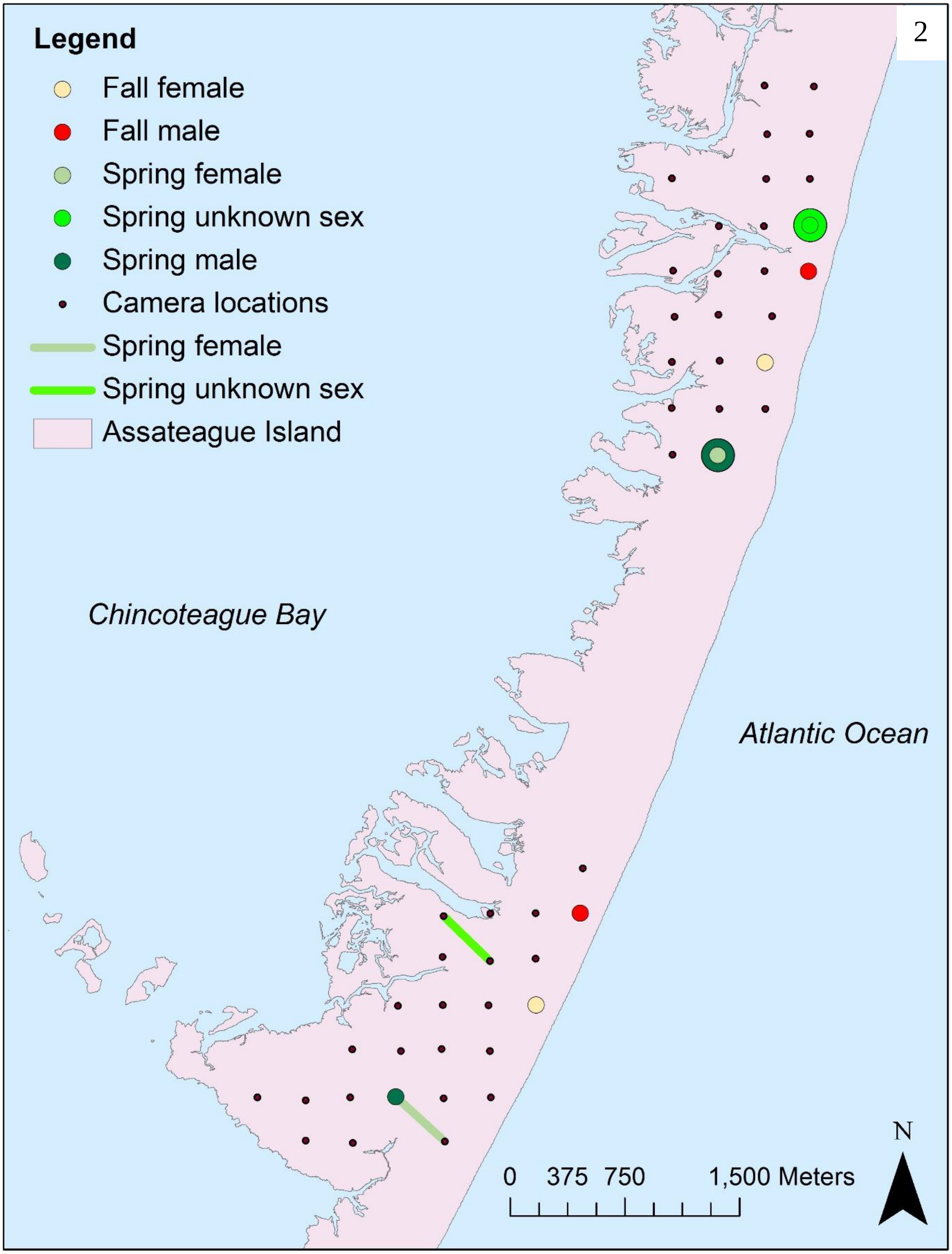

2014-03-10 6:51:50 AM M 1/5
34°F
RECONYX

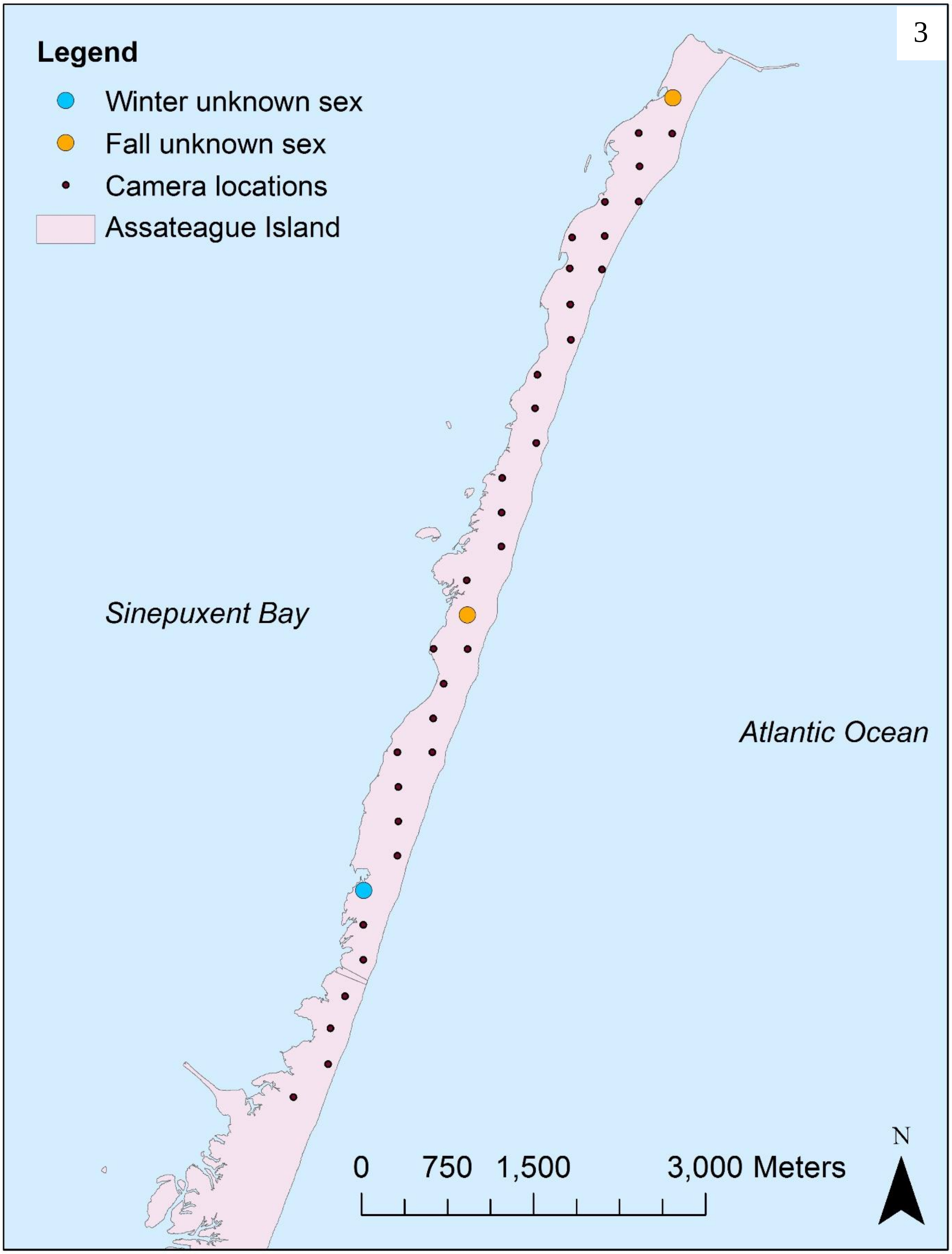
4

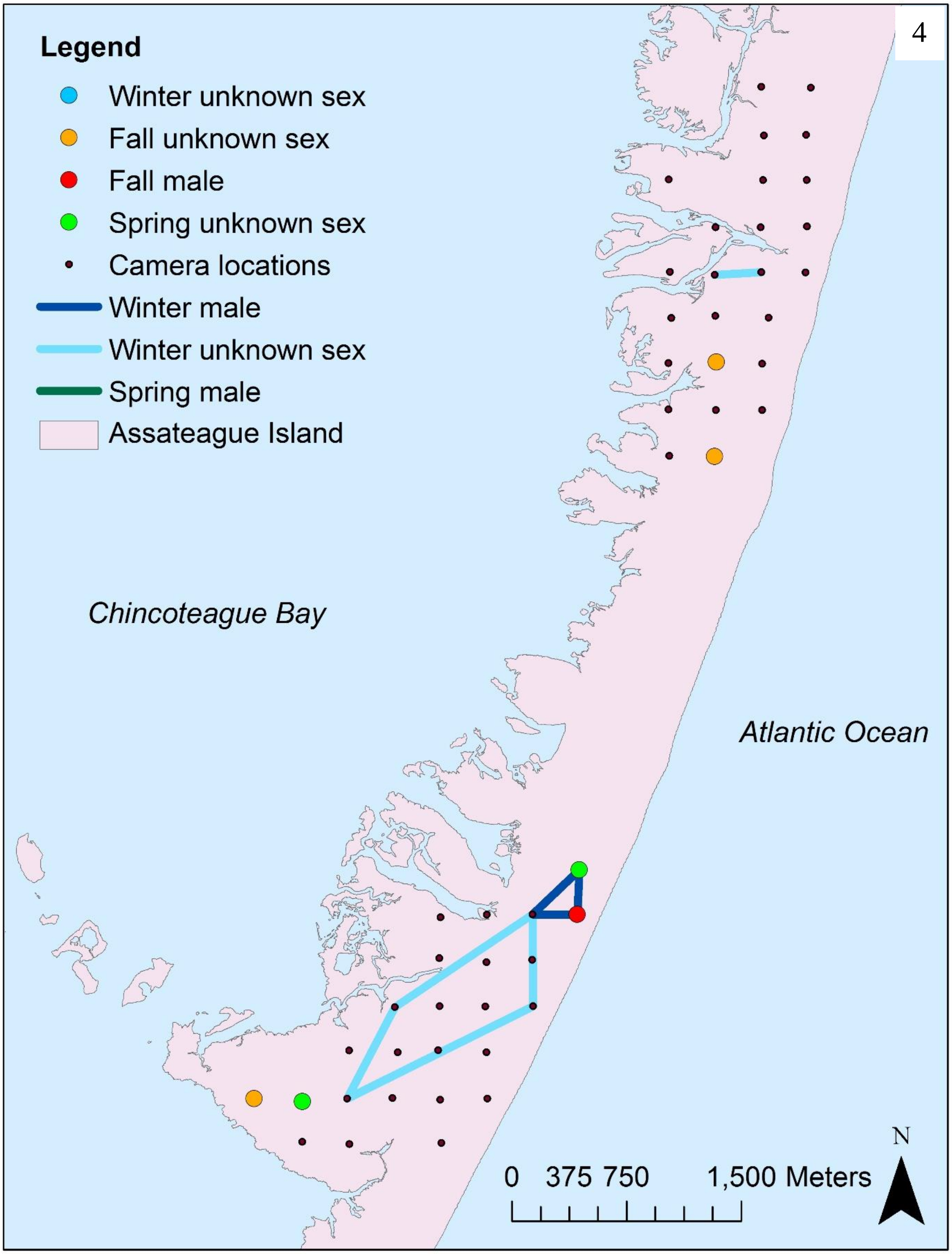

2014-03-25 10:37:16 AM M 1/5
41°F
WIPL30.NEST
RECONYX

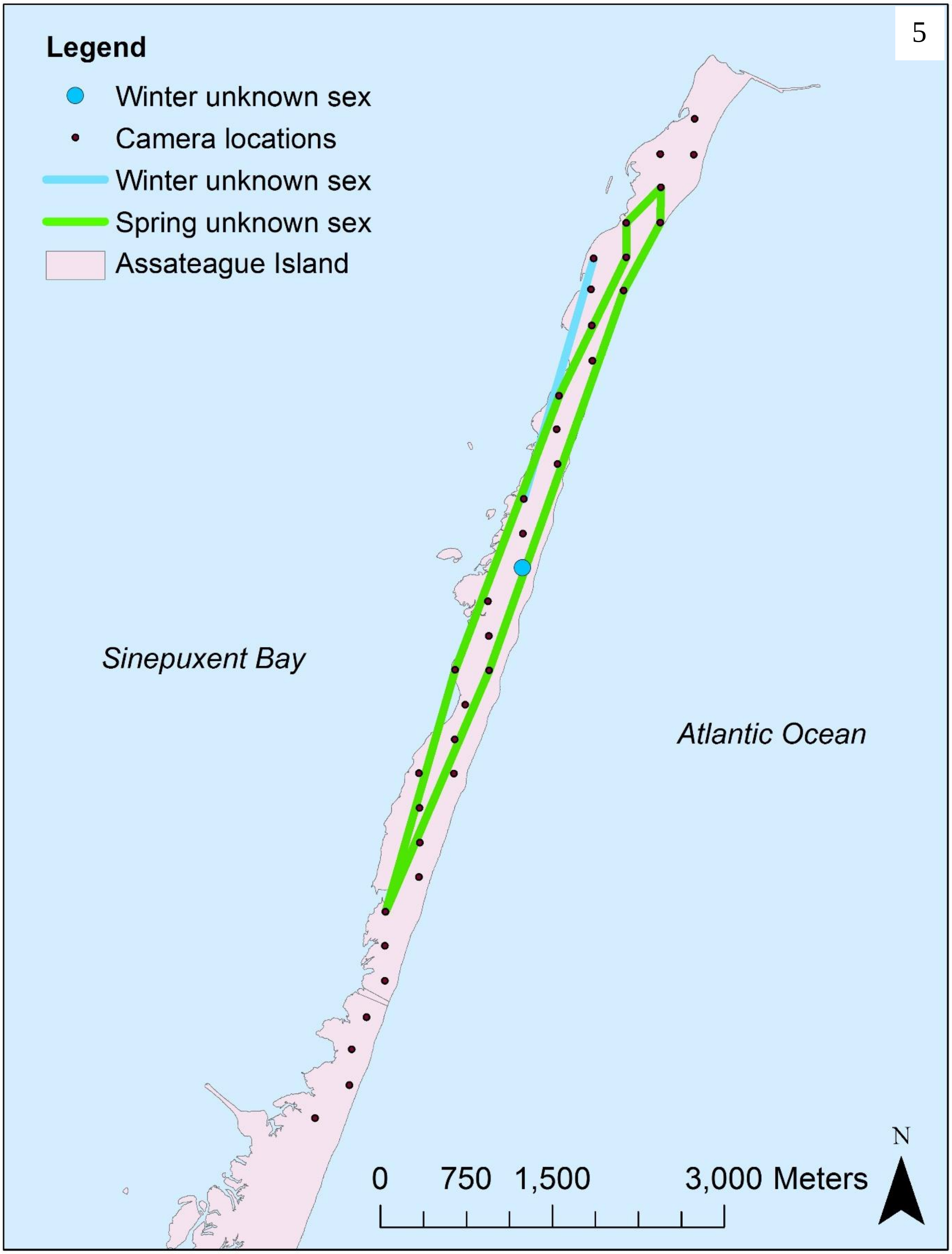
S7. Example of an individual red fox (*Vulpes vulpes*) identified using unique characteristics. This individual was identified by a uniquely white/light forehead and dark patches on its hind limbs. This individual was recaptured 9 times and was captured at 7 different camera stations. This individual was also identified as a male by the scrotum visible in Plate 4.

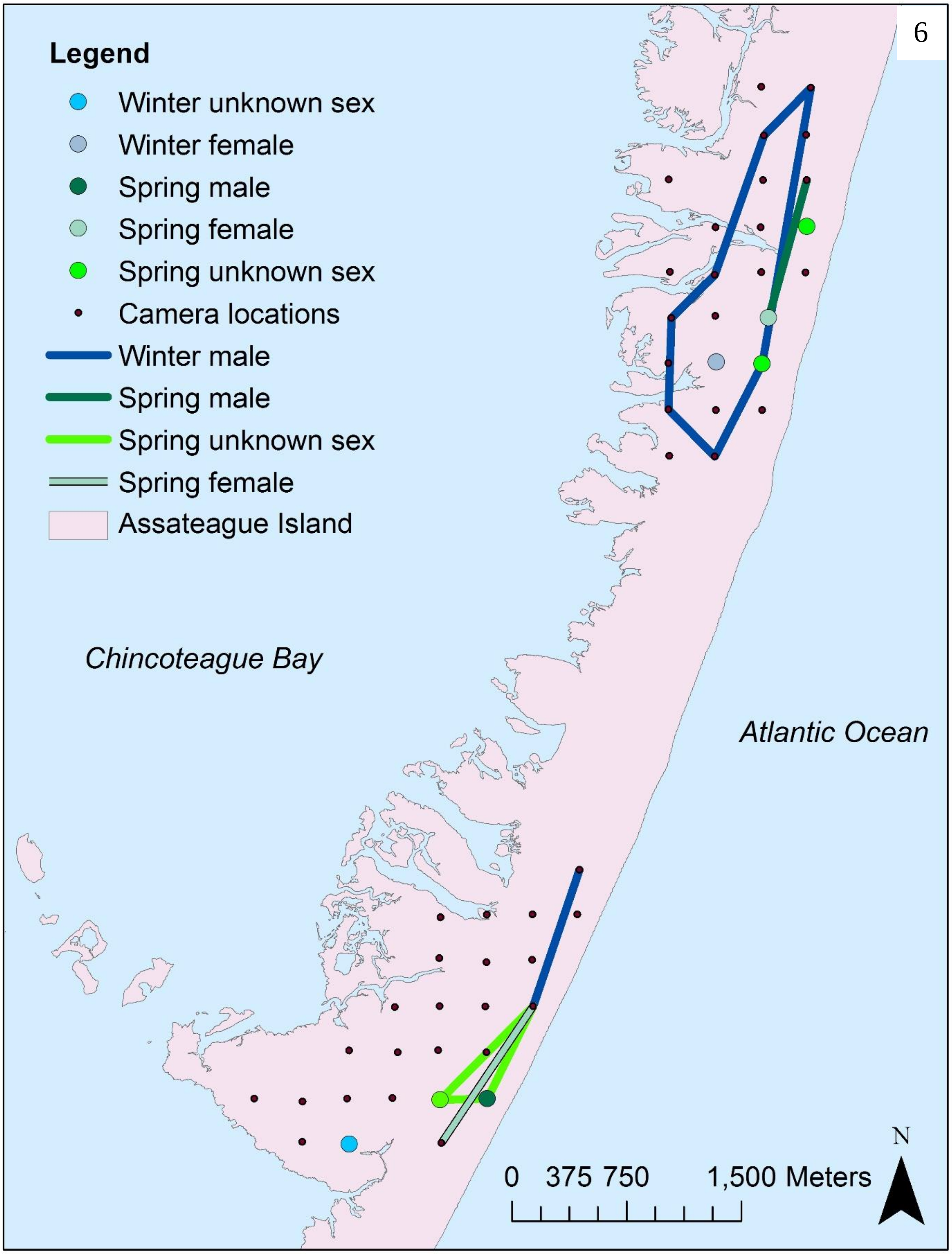

1
Legend
Fall female
Fall male
Spring female
Spring unknown sex
Spring male
Camera locations
Spring female
Spring unknown sex
Assateague Island
Sinepuxent Bay
Atlantic Ocean
0
750
1,500
3,000 Meters
N


2
Legend
Fall female
Fall male
Spring female
Spring unknown sex
Spring male
Camera locations
Spring female
Spring unknown sex
Assateague Island
Chincoteague Bay
Atlantic Ocean
0
375
750
1,500 Meters
N


3
Legend
Winter unknown sex
Fall unknown sex
Camera locations
Assateague Island
Sinepuxent Bay
Atlantic Ocean
0
750
1,500
3,000 Meters
N


4
Legend
Winter unknown sex
Fall unknown sex
Fall male
Spring unknown sex
Camera locations
Winter male
Winter unknown sex
Spring male
Assateague Island
Chincoteague Bay
Atlantic Ocean
0 375 750 1,500 Meters
N


5
Legend
Winter unknown sex
Camera locations
Winter unknown sex
Spring unknown sex
Assateague Island
Sinepuxent Bay
Atlantic Ocean
0
750
1,500
3,000 Meters
N


Legend
Winter unknown sex
Winter female
Spring male
Spring female
Spring unknown sex
Camera locations
Winter male
Spring male
Spring unknown sex
Spring female
Assateague Island
Chincoteague Bay
Atlantic Ocean
0 375 750 1,500 Meters
N

6

S8. Maps showing camera station locations and individual red fox movements for males, females, and unknown sex in spring and winter at three camera grids (A, B, C) from (2012–2014) at Assateague Island National Seashore, MD. Continuous lines represent one individual that was seen at multiple camera stations. Dots represent individuals that were only seen at one camera. Movements in 2012 are shown in Plates 1 (Grid A) and 2 (Grids B and C running North to South). Movements in 2013 are shown in Plates 3 (Grid A) and 4 (Grids B and C running North to South). Movements in 2014 are shown in Plates 5 (Grid A) and 6 (Grids B and C running North to South).

CHAPTER 6

THE ROAD AHEAD: CONSERVING PIPING PLOVERS (*CHARADRIUS MELODUS*) IN THE FACE OF RISING SEAS AND PERSISTENT PREDATION THREATS

Introduction

The piping plover (*Charadrius melodus*) has and will continue to maintain high profile status as a threatened species on the U.S. Atlantic Coast for the foreseeable future; however, it is also an example of how well-planned and well-implemented management can lead to conservation success. Dedicated efforts to conserve this species have substantially increased their population numbers since they were listed under the Endangered Species Act in 1986, from 790 pairs at listing in the U.S. Atlantic Coast breeding subpopulation to 1,782 pairs in 2010. Efforts focused on piping plovers also benefit other imperiled species that depend on these same coastal habitats, 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*), Northeastern beach tiger beetles (*Cicindela dorsalis dorsalis*), loggerhead (*Caretta caretta*) and green (*Chelonia mydas*) sea turtles, and seabeach amaranth (*Amaranthus pumilus*; USFWS 1996, Hecht and Melvin 2009a). The ultimate goal of all federally-listed species recovery plans is to increase a species population to a sustainable level. For the piping plover, achieving this goal will require sustained conservation efforts until and after it is delisted, particularly for plovers breeding along the Atlantic Coast whose breeding habitat along sandy beaches is highly coveted as prime recreational and vacation destinations (Crowell et al. 2010, Zhang and Leatherman 2011).

Persistent threats to piping plovers along the U.S. Atlantic Coast, which will require continued management to reach and then maintain the recovery goal of 2000 pairs of piping plovers, include changes to breeding habitat due to human development and sea-level rise, human disturbance, and predation (USFWS 1996, Clark and Niles 2000, Hecht and Melvin 2009b). Despite much research that has contributed to the success of current piping plover recovery efforts, significant gaps remain, particularly with regards to our understanding of how plovers will respond to climate change and human-mediated changes in their coastal habitats, how their predators use coastal habitat, and in turn, how predator habitat relates to breeding shorebird productivity (USFWS 1996). Although future research needs continue, as I outline below, my dissertation research contributed significant information to fill in these gaps. The goals of my research, outlined in the preceding chapters were to 1) develop and implement a tool to predict future change to piping plover habitat resulting from sea-level rise and beach management efforts, and 2) address gaps in our understanding of shorebird mammalian predator population ecology, in particular red foxes (*Vulpes vulpes*) which are a predator of management concern on Assateague Island, Maryland where my study was conducted and in many locations throughout the U.S. Atlantic Coast breeding population.

To address my goal of developing a tool to predict future climate change-induced alterations to piping plover nesting habitat, we built a predictive model using a dataset collected at Assateague Island on piping plover nest locations, random points, and physical features from nest and random points in 1999, 2002, and 2008. We developed and tested this model initially using data from nests in 1999, 2002, and 2008, and then linked this model to a geomorphology and shoreline change model to predict changes to nesting habitat suitability in the next 50-100 years under several sea-level rise and beach management scenarios.

To address my goal of aiding our understanding of shorebird mammalian predator population ecology, we used photographic sampling to survey mammalian predators at Assateague Island National Seashore (ASIS), on the Maryland portion of Assateague Island, from 2012-2014. We conducted surveys across three camera grids in ASIS over three seasons and two years: spring (April to June), fall (August to October), and winter (January to March). We surveyed a total of 539 days, providing a total of 22,628 trap nights (mean = 7,543 ± 620 SD per camera grid). These surveys provided a total of 37, 399 photographic captures of mammals, from which we identified 11 species, including 4 carnivores (red fox, raccoon *(Procyon lotor*), North American river otter (*Lontra canadensis*) and Virginia opossums *(Didelphis virginiana*).

I summarize below my major findings, management implications, and future research needs from my work described in this dissertation.

Major findings

Goal 1: develop and implement a tool to predict future change to piping plover habitat resulting from sea-level rise and beach management efforts

- model predictions were more successful when the ranges of physical variables in the model were varied rather than narrow
- our model correctly predicted suitable nesting habitat better than unsuitable nesting habitat
- modest sea-level rise rates may increase suitable piping plover nesting habitat area in 50–100 years and some beach management strategies influence habitat availability

Goal 2: address gaps in our understanding of shorebird mammalian predator population ecology, in particular red foxes which are a predator of management concern on Assateague Island, MD and throughout the U.S. Atlantic Coast piping plover breeding populations

- red fox occupancy was strongly tied to eastern cottontail (*Sylvilagus floridanus*) trap success, increasing sharply with increased eastern cottontail trap success

- red fox occupancy did not change in response to an intensive eradication program on the northern section of the island
- red foxes on ASIS moved on average more in the spring and winter seasons than in the fall, and movements across all seasons averaged 302.4 m and ranged 0-6,752.4 m; the largest movement observed (6,752.4 m) occurred after lethal removal of foxes from the North End of Assateague Island and suggests that foxes may have limited movements and exist in fairly stable territories, but large movements are possible and may occur when lethal removal opens up formerly occupied territories

Management implications and future research needs

Our development and implementation of a tool to predict change in piping plover habitat suitability provides a vital starting point for predicting how plover nesting habitat will change in a context of planned human modifications intended to address climate change-related threats (USFWS 2009). Further analyses under varying beach management scenarios should show the implications for nesting plovers, thus informing managers considering various beach management options for piping plovers and other species that are dependent on coastal ecosystems. This plover habitat suitability model will be applicable to managers coast-wide, and is currently being tested and expanded to other plover nesting locations, including sites from Massachusetts to North Carolina.

Our findings regarding red fox occupancy and movement provide important information on the effects of certain predator management activities and habitat use of a key mammalian predator for shorebirds along the U.S. Atlantic Coast. The lack of effect we found of lethal removal efforts on red fox occupancy and movement should be investigated on other barrier islands, as this finding has important ramifications for the sustainability of sustained predator removal programs. Furthermore, the positive relationship we found between red foxes and eastern cottontails has important implications for future effects of habitat change on this predator.

Future research should integrate predictions of habitat change on both plovers and their predators. Feedback loops that model the connection between species at multiple levels should be incorporated into models of future change. Our findings provide guidance on what components should be incorporated in feedback loops, for example how vegetation changes affect eastern cottontails, how resulting fluctuations in eastern cottontails affect red fox occupancy, and how consequential changes in red fox occupancy affect plover breeding productivity. Our predictive model and predator occupancy and movement findings, combined with future research aimed at further refining predictions of future change will allow wildlife managers to better plan and implement effective management actions for piping plovers in response to the multiple stressors of SLR-induced habitat change and predation.

Literature cited

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