

**FACTORS AFFECTING PIPING PLOVER (*CHARADRIUS MELODUS*) NEST SITE
SELECTION FOLLOWING LANDSCAPE AND PREDATOR COMMUNITY
CHANGES**

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ACADEMIC ABSTRACT

The dynamics of coastal landscapes following major storm events and human interventions significantly impact nesting habitat use by species like the piping plover (*Charadrius melodus*) along Atlantic coastlines. Our study focused on Fire Island, New York, assessing changes in vegetation succession, plover nesting habitat selection, and suitable nesting habitat availability from 2010 until eight years after Hurricane Sandy. We analyzed classified imagery to quantify vegetative cover changes across the landscape and at nest sites. Results showed an increase of 11.5% change in vegetative cover across the study area, and nest sites experienced an increase in vegetation cover from 0.1% to 6.2% between 2015 and 2020. Selection for four habitat variables (i.e., distance to ocean, least-cost distance to bay, elevation, backshore width) was consistent throughout the study, but post-hurricane nests were situated farther from development and closer to bay areas (Euclidean distance) compared to pre-hurricane. Moreover, suitable nesting habitat peaked immediately post-stabilization but declined in subsequent years. Understanding these landscape shifts provides insights into species prioritization of habitat characteristics during nesting. Piping plovers face predation threats during breeding seasons while balancing consideration of the aforementioned habitat considerations, leading to specific nest placement strategies. Our study examined the relationship between nest site selection and the area visible from nests (viewshed) and evaluated its addition in nest site selection models including habitat variables. Piping plovers exhibited a preference for nest sites with increased predator visibility

compared to random selection, indicating a strategic selection process. Initially influential ($\beta = 0.43$; CI = 0.28 – 0.58), the role of this predator visibility ('viewshed') diminished ($\beta = -0.13$; CI = -0.23– -0.04) as the landscape underwent ecological succession. Topographic variation caused greater visual obstruction at nest sites than vegetation. This study on piping plovers offers insights into the interaction between landscape changes, habitat selection, and predator visibility. The evolving importance of viewshed in nest site selection underscores the dynamic nature of nesting strategies in response to changing environments, and incorporation of this variable can improve the predictive ability of other models as it did for this study. These findings have broader implications for ground-nesting bird species and highlight the importance of considering landscape changes and predator visibility in land management strategies to safeguard vulnerable avian populations.

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GENERAL AUDIENCE ABSTRACT

This is a study of piping plover (*Charadrius melodus*) nesting behaviors and nesting habitat conditions on Fire Island, New York prior to and following Hurricane Sandy in 2012. Over a decade, our observations documented remarkable alterations in both the landscape and nesting preferences of these birds. Vegetation that was initially covered by overwashed sand from the storm re-emerged in many areas across the study area and reduced the amount of suitable nesting habitat for plovers. Although some factors consistently influenced nesting site selection, after Hurricane Sandy, plovers nested farther from human development and closer to the coastal bay. Moreover, our investigation extended to understanding how these birds strategically choose safe nesting grounds with optimal visibility to potential predators. Initially, plovers nested in areas with greater visibility of predators, but as the landscape experienced vegetation succession nest-site viewshed became less of a priority. We also documented sources of visual obstruction at nests and determined that the topographic features obstructed more area than vegetation; however, sand captured by vegetation contributes to hummocks and dune creation. These findings illuminate the adaptability of piping plover nesting behaviors in response to the changing landscapes. Understanding how the environment changes and how animals adapt to these changes is crucial for creating strategies to protect vulnerable bird populations like piping plovers in coastal areas.

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“In the end, we conserve only what we love.

We love only what we understand.

We will understand only what we are taught.”

Baba Dioum

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ATTRIBUTIONS

The following summarizes the contributions made by coauthors to these manuscripts.

Chapter 1. Post-hurricane habitat changes and the long-term behavioral response by a barrier island shorebird: the piping plover (*Charadrius melodus*)

James Fraser (Department of Fish and Wildlife Conservation, Virginia Tech) and Daniel Catlin (Department of Fish and Wildlife Conservation, Virginia Tech) secured funding, contributed to study design, provided analytical support, and substantially edited the manuscript. Shannon Ritter (Department of Fish and Wildlife Conservation, Virginia Tech) provided GIS analytical support. Samantha Robinson (Department of Fish and Wildlife Conservation, Virginia Tech) collected data, provided analytical support and substantially edited the manuscript. Katie Oliver (Department of Fish and Wildlife Conservation, Virginia Tech) and Henrietta Bellman (Department of Fish and Wildlife Conservation, Virginia Tech) collected data. Christy Wails (Department of Fish and Wildlife Conservation, Virginia Tech) provided substantial analytical support and edited the manuscript. Sarah Karpanty (Department of Fish and Wildlife Conservation, Virginia Tech) provided support and substantially edited the manuscript.

Chapter 2. Head on a swivel: the importance of viewshed in nest site selection of a ground nesting bird

James Fraser (Department of Fish and Wildlife Conservation, Virginia Tech) secured funding and substantially edited the manuscript. Daniel Catlin (Department of Fish and Wildlife Conservation, Virginia Tech) secured funding, contributed to study design, provided analytical support, and substantially edited the manuscript. Sarah Karpanty (Department of Fish and Wildlife Conservation, Virginia Tech) provided support and substantially edited the manuscript.

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INTRODUCTION

Barrier islands are thin strips of land between the ocean and the mainland that undergo repeated cycles of coastal disturbance and ecological succession, with retreat facilitated by storm-induced overwash or landward sand movement (Dolan et al. 1980, Oertel 1985, Morton and Jr. 2003, Roelvink et al. 2009, Burvingt et al. 2016, Enwright et al. 2021). Anthropogenic modifications, such as coastal hardening or beach nourishment, can disrupt natural processes, potentially slowing or exacerbating erosion (Kraus 1988, Peterson and Bishop 2005). With climate change posing a threat to coastal regions, there is growing emphasis on engineered stabilization of barrier islands (Feagin et al. 2010a, Helderop and Grubestic 2019). However, the features that make these islands susceptible to breaching—low elevation, narrow width, regions without dunes—also are crucial habitats for coastally-adapted species. In fact, certain species are dependent on post-disturbance landscapes created from storm and flooding events (Davis et al. 2001, Minchinton and Bertness 2003, Fraser and Catlin 2019, Robinson et al. 2019).

In periods of little to no disturbance on barrier islands, particular species of coastal vegetation thrive, and ecological succession occurs (Burrows 1990). Pioneer species like beach grasses establish on bare sand dunes and trap wind-blown sand over time, gradually creating a more hospitable environment for larger plant species (Miller et al. 2001, Isermann 2011). American beachgrass (*Ammophila breviligulata*) is the key player in re-establishing plant communities following disturbances (Cheplick 2016). Over time, the interplay between plant communities and dune systems naturally stabilize the shoreline (Miller et al. 2001, Feagin et al. 2015a), which provides habitat for several coastal animal species.

One such barrier island system is Fire Island, New York, whose beaches support a variety of vertebrates including mammalian species such as the raccoon (*Procyon lotor*), muskrat

(*Ondatra zibethicus*), Eastern cottontail (*Sylvilagus floridanus*) and red fox (*Vulpes vulpes*; Trocki 2010, Peterson et al. 2021), and avian species like the roseate tern (*Sterna dougallii*), saltmarsh sparrow (*Ammodramus caudacutus*), laughing gull (*Leucophaeus atricilla*), and piping plover (*Charadrius melodus*, hereafter ‘plover’; Bull and Farrand 1994). The plover is a federally threatened shorebird (USFWS 1985, Hecht et al. 1996) that annually migrates to northern shorelines (including Fire Island, New York) for the breeding season and are one of the species that benefit from occasional disturbance to their habitat (Robinson et al. 2019).

On 29 October 2012, Hurricane Sandy hit the mid-Atlantic coast of the United States causing substantial changes to the landscape of the New York barrier islands (Sopkin et al. 2014). The storm surges and wave action uprooted deep-rooted plants, depositing sediment within the bay to form flood shoals, while also flattening dunes and resetting the landscape to an earlier stage of ecological succession. Following the storm, the U.S. Army Corps of Engineers proposed the Fire Island Inlet to Moriches Inlet Stabilization Project (FIMI), aimed at mitigating the potential consequences of significant storms on coastal communities to enhance coastal risk reduction. Under Section 7 of the Endangered Species Act, the U.S. Fish and Wildlife Service developed a Biological Opinion for the FIMI project's potential impact on breeding piping plovers, outlining habitat creation and management goals (USFWS 2014). In accordance with the Biological Opinion, approximately 45 hectares of restoration area was established during late 2014 to imitate overwash habitat and mitigate the loss of plover breeding habitat resulting from the stabilization project (i.e., FIMI; USACE 2014). Further modifications prioritizing shoreline stabilization included activities such as dune creation, beach nourishment, and vegetation planting. After a couple of years of regular disturbance from construction machinery between

2012–2014, the plover nesting habitats across the island were left largely undisturbed, restarting the cycle of ecological succession (Burrows 1990).

In addition to the change in the physical landscape, the biological landscape also experienced changes shortly after completion of the FIMI projects. As a result of a sarcoptic mange outbreak, a transmittable infestation of mites on the body causing hair loss and severe irritation, the red fox population was extirpated from Fire Island in 2015 (within the eastern region) and 2017 (within the western region; Black 2021). With the loss of a top predator, it was hypothesized that populations of mesopredators, the trophic level below the top predator, would surge, a process called ‘mesopredator release’ (Prugh et al. 2009). An increase in other mammalian predators, such as raccoon and cat (*Felis catus*), was noted on the landscape in the years without red fox presence (Black 2021). Red fox were regarded as a primary predator of the plover (Cohen et al. 2009, Hunt et al. 2019), while raccoon and cats also were noted to depredate specific life stages of the bird (Hunt et al. 2019). To defend themselves, their chicks, or their nests against these predators, adult plovers exhibit antipredator behavior in the form of the ‘broken-wing display’(de Framond et al. 2022). Effective use of this defensive tactic only is possible with appropriate timing between threat detection and deploying the behavior, particularly during the incubation stage.

Plovers are federally listed as threatened (Atlantic Coast and Great Plains populations) and endangered (Great Lakes population) under the Endangered Species Act (USFWS 1985) in part due to the loss of open and sparsely vegetated habitat throughout its range (Wilcox 1959, Elliott-Smith and Haig 2020). Because of their population status, plovers have been extensively studied and monitored over several decades (Wilcox 1959, Prindiville Gaines and Ryan 1988, Cohen et al. 2009, Fraser and Catlin 2019). Conservation initiatives have focused on habitat

preservation, predator management, and public awareness to mitigate human disturbance at nesting sites (Hecht et al. 1996, Hecht and Melvin 2009, Cavalieri et al. 2020). Despite these efforts, piping plover populations remain precarious, with ongoing threats from coastal development, recreational activities, and climate change. Continued conservation measures, including habitat restoration and coordinated management, are crucial to ensure the long-term survival of this species (Melvin et al. 1991, Hecht et al. 1996, Cavalieri et al. 2020).

Conservation of this threatened species comes from understanding behavioral choices – especially during the nesting stage. Plovers are a beach-nesting bird, and researchers have long investigated their nest site selection behaviors in variety of landscape conditions within New York (Burger 1987, Cohen et al. 2008, Walker et al. 2019) and beyond (Espie et al. 1996, Gieder et al. 2014, Grant et al. 2019, Zeigler et al. 2021). Plovers are described as ‘disturbance-dependent’ because of their need for periodic disturbance on their breeding grounds, responding relatively rapidly to habitat changes. Thus, plovers are an ideal species to study responses to changes in barrier island habitat (Gieder et al. 2014, Zeigler et al. 2017, Robinson et al. 2023). Nest site selection in plovers is driven by trade-offs to maximize access to foraging areas and minimize competition, predation, and flooding (Fraser and Catlin 2019). Typical landscape features investigated in nest site selection studies have included distance to foraging areas (Loefering and Fraser 1995a, Elias et al. 2000), distance to dunes (Burger 1987, Maslo et al. 2011), distance to vegetation (Burger 1987), and ground elevation (Walker et al. 2019).

Plover breeding habitat management can be challenging because their nesting behavior is not constant, which may be reflective of the intrinsic, dynamic nature of shorelines they nest on. Variation in selected nesting sites has been noted across latitudes (Zeigler et al. 2021) and following significant habitat change at their breeding grounds (Walker et al. 2019). Long-term

studies provide a unique opportunity to evaluate behavior change or consistency when the landscape changes. Before Hurricane Sandy, Fire Island plovers were found to select nest sites farther from the ocean and bay intertidal than would be expected at random, selecting areas in the mid-island backshore (Walker et al. 2019). Post-Hurricane Sandy, plovers selected nest sites closer to the bay intertidal zone than would be expected at random (Walker et al. 2019). We examined selection for previously studied variables (e.g., distance to bay, distance to development, elevation) under the context of landscape change from ecological succession. In addition to the aforementioned variables, we also explored ‘viewshed’ – the view of one’s surroundings – to assess if achieving visibility of ground predators from the nest is a factor in nest site selection.

The overall goals of this thesis research were to:

1. Describe the influence of several habitat variables on nest site selection over time as the landscape underwent ecological succession and assess changes in the amount of suitable plover nesting habitat during different landscape stages (Chapter 1).
2. Evaluate the role of viewshed on plover nest site selection in the context of a shifting predator community and identify the primary source of visual obstruction on the landscape (Chapter 2).

The specific objectives of Chapter 1 were to examine plovers’ response to ecological succession-induced habitat change by 1) estimating the percentage of vegetation cover across the study area and within nest sites immediately after the hurricane (2013–2014), after island stabilization (2015), and in years with unmodified vegetation growth (i.e., natural succession; 2016–2020), 2) using logistic regression to assess the effect of six geospatial habitat

characteristics on plover nest site selection before the hurricane (2010) and after (2015–2020), and 3) quantifying the amount of suitable nesting habitat available to plovers before the hurricane (2010), after island stabilization (2015), and following years of ecological succession (2020) based on geospatial habitat characteristics selected by nesting plovers.

In Chapter 2, our main objectives were to 1) compare the effectiveness of two viewshed scenarios (i.e., detecting larger predators and all terrestrial predators) for predicting nest site selection and examine how predator detectability influenced selection in the years post-island stabilization, 2) assess if incorporating viewshed enhances the predictive ability of a model evaluating nest site selection along with six other habitat variables, 3) interpret model of selection, including a viewshed and years since storm interaction, to gauge the ongoing importance of viewshed in nest site selection amid landscape changes, and 4) analyze the relative impact of vegetation and topography on obstructing the viewshed at plover nests by comparing the visible area at nest sites with the isolated effect of each obstruction source.

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**CHAPTER 1: POST-HURRICANE HABITAT CHANGES AND THE LONG-TERM
BEHAVIORAL RESPONSE BY A BARRIER ISLAND SHOREBIRD: THE PIPING
PLOVER (*CHARADRIUS MELODUS*)**

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Post-hurricane habitat changes and the long-term behavioral response by a barrier island shorebird: the piping plover (*Charadrius melodus*)

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Abstract

Changes in coastal landscapes from major storm events and the anthropogenic modifications that may follow (e.g., beach stabilization) affect processes like overwash and the regeneration of dunes and vegetation. These processes in turn influence the nesting habitat use of the piping plover (*Charadrius melodus*), which breeds on Atlantic coast shorelines. We studied vegetation succession, plover nesting habitat selection, and the availability of suitable nesting habitat on Fire Island, New York, in 2010, and in years following Hurricane Sandy (2013–2020). We classified aerial imagery by land cover type to determine the amount of vegetative cover across the study area and at nest sites annually, evaluated a generalized linear model with six previously assessed habitat variables for shifts in pre-hurricane vs post-hurricane nest site selection, and modeled suitable nesting habitat in 2010 (pre-hurricane), 2015 (post-stabilization), and in 2020 (post-succession). From 2015–2020, vegetative cover across the landscape increased by 11.5%, and the median vegetative cover at nest sites increased from 0.1% to 6.2%. Post-hurricane selection for four habitat variables (backshore width, elevation, distance to ocean, and least-cost distance to bay) was similar to pre-hurricane selection; however, post-hurricane nests were farther from development and closer (Euclidean distance) to bay habitats than pre-hurricane. Lastly, the amount of suitable nesting habitat peaked in the post-stabilization period and declined in the post-succession period. Long-term evaluation of species' response to landscape changes

offers greater insight into the prioritization of nesting habitat characteristics and any fluctuation in criteria used to determine suitable nesting habitat.

Keywords: nest-site selection, shoreline, suitable habitat, vegetation succession, use-versus-availability

1. Introduction

Many western Atlantic and Gulf of Mexico coastlines are fringed by barrier islands, thin strips of land situated between the ocean and mainland (Dolan et al. 1980, Oertel 1985, Stutz and Pilkey 2001). Barrier islands are reshaped continuously by wind, waves, and tides (Davis, Jr. and Fitzgerald 2009, Feagin et al. 2015*b*), which cause sediment to accrete or erode depending on the conditions (Morton et al. 1995). During storms, barrier islands may change substantially in hours or days (Passeri et al. 2018). Dunes may be leveled, vegetation may be buried or scoured away, and sand, shells, and wrack may be deposited on the beach. Islands can also be breached leaving temporary or semi-permanent inlets (Roelvink et al. 2009, Burvingt et al. 2016).

Coastal engineers are often tasked to stabilize barrier island shorelines to protect human infrastructure (Kraus 1988, Peterson and Bishop 2005). Stabilization projects may include beach renourishment (depositing dredged benthic substrate), construction of jetties or groins (boulders placed perpendicular to the longshore current), and vegetation planting (Rotimi et al. 2009, USACE 2014). Considering the anticipated increase in storm frequency and flooding from sea level rise (Little et al. 2015, Holle et al. 2019), coastal engineering projects are likely to increase. However, these islands provide habitat for many plant and animal species (Dolan et al. 1980, Feagin et al. 2010), and habitat suitability for species may be altered as a result of engineering actions (e.g., Walker et al. 2019, Gutierrez et al. 2022).

More than 30 shorebird species use U.S. barrier islands for breeding, wintering, or migrating (Brown et al. 2001) including red knots (*Calidris canutus*), American oystercatchers (*Haematopus palliatus*), and piping plovers (*Charadrius melodus*; hereafter ‘plovers’). These species forage on polychaetes, crustaceans, and bivalves in barrier island intertidal zones and tidal flats (Cohen et al. 2010, Heller et al. 2022). Many barrier islands are remote and devoid of significant human disturbance, which makes them more hospitable to shorebirds (Burger and Niles 2013, Schlacher et al. 2013, Gibson et al. 2018). Unvegetated sandy washovers are used for nesting and roosting (Withers 2002). Increased nesting habitat can release habitat-limited populations (Robinson et al. 2019). For example, Hurricane Sandy increased the dry sand available for plover nesting in a New York study area 1.5-fold, and the plover population increased by 93% (Walker et al. 2019). However, habitat gains after storms can quickly be lost to vegetative and geomorphic succession.

In the absence of storms, however, specific coastal plants flourish and initiate the process of ecological succession on the landscape (Burrows 1990), limiting the available nesting habitat for plovers (Robinson et al. 2019). Beach grasses and other pioneer species establish themselves on bare sand dunes, capturing wind-blown sand, thereby progressively creating habitat for larger plants (Miller et al. 2001, Isermann 2011, Cheplick 2016). Increasing vegetation cover can displace adult plovers who typically select unvegetated or sparsely vegetated nesting sites (Cairns 1982, Cohen et al. 2008), and potentially disadvantageous to flightless chicks whose route to foraging areas might be impeded by dense vegetation (Walker et al. 2019, Robinson et al. 2021).

Here, we examine the uninterrupted ecological succession following Fire Island stabilization and plovers’ response to this habitat change by 1) estimating the percentage of

vegetation cover across the study area and within nest sites immediately after the hurricane (2013–2014), after island stabilization (2015), and during years of unimpeded vegetation succession (2016–2020), 2) using logistic regression to assess the effect of six geospatial habitat characteristics on plover nest site selection before the hurricane (2010) and after (2015–2020), and 3) measuring the amount of suitable nesting habitat available to plovers before the hurricane (2010), after island stabilization (2015), and following years of ecological succession (2020) based on the geospatial habitat characteristics selected by nesting plovers.

2. Methods

2.1 Study area

We assessed aspects of plover nesting habitat and nesting behavior on Fire Island, New York, USA (40.710604°N, -72.931583°W; Fig. 1) in 2010 and 2013–2020. Fire Island is a 24.8-km long and 0.4-km wide barrier island south of Long Island, New York and is bounded by the Great South Bay and other bays to the north and the Atlantic Ocean to the south. We surveyed beaches within Robert Moses State Park, Fire Island National Seashore's Otis Pike Wilderness Area and Lighthouse Beach, and Smith Point County Park (Fig. 1).

Specific barrier islands' geological zones vary but exhibit similarities across different systems. (Leatherman 1979, Dolan et al. 1980, Oertel 1985). The study area comprised four distinct zones: backshore, primary dune, interdune, and bayside. Vegetation varied across these zones, with little to no vegetation within the backshore, grasses on the primary dune, shrubs dominating the interdune area, and the bayside habitat consisting of marshes, sparse shrubs, forest patches, or open sandy intertidal area. Common vegetation on Fire Island included American beachgrass, common reed (*Phragmites australis*), seaside goldenrod (*Solidago*

sempervirens), beach pea (*Lathyrus japonicus*), and wooly beachheather (*Hudsonia tomentosa*; Bellman 2018). Some beach regions bordered developed areas (e.g., paved parking lots and visitor facilities).

2.2 Hurricane Sandy

Hurricane Sandy reached the shore as a Category 1 storm on 29 October 2012 near Brigantine, New Jersey, where severe dune erosion and breaches allowed waves to carry sand inland (Sopkin et al. 2014). The storm left significant impact on neighboring regions as well. Dunes along Fire Island lost as much as 5 m of elevation, associated with substantial overwash that further flattened the beach topography and buried vegetation. This overwash also led to significant sand transport inland, property damage, and breaches at various locations, including Old Inlet.

Fire Island gained approximately 72 ha of dry sand for plover nesting and approximately 2 km of bayside intertidal foraging habitat from the newly flattened areas created from the storm's overwash events (Walker et al. 2019). In 2015, the U.S. Army Corps of Engineers (USACE) oversaw construction of two restoration areas, creating an additional 39.7 ha of dry sand habitat within the study area (USFWS 2014, USACE 2014). During this time, the overwashed areas consisted of sparse, low-lying vegetation in its early successional stage, but due to the lack of major storms in the following years, ecological succession has proceeded unimpeded throughout these regions.

2.3 Field methods

We acquired 2010 nest location data from local land managers and began the post-hurricane nest monitoring in 2015. We conducted nest searching from April to July in 2015–

2020 in all potential nesting habitats across the study area including backshore (i.e., from the ocean shoreline to dune line), interior (i.e., between dune line and bay shoreline), and vegetated areas. We searched for nests within the study area every 1–3 days by walking transects and observing adult plover behavior. We recorded nest coordinates using a Trimble Geo7x GPS unit (Trimble, Sunnyvale, California, USA). In 2020, due to COVID-19, we obtained nesting data from land managers.

2.4 Geospatial analysis methods

We acquired fine-scale (15-cm resolution) aerial imagery each April 2010, 2013–2020 (Axis Geospatial, Easton, MD, USA), and used the ‘Maximum Likelihood Classification’ tool in ArcMap 10.6 (Esri Inc., Redlands, CA, USA) to classify the imagery’s pixels as dry sand, wet sand, vegetation, or water. To quantify vegetation succession in the years following the hurricane, we counted the pixels classified as vegetation in each year within the study area and within 30 m of plover nest sites.

Plovers often select nest sites with access to forage in ocean and bay intertidal zones (Loefering and Fraser 1995*b*, Elias et al. 2000, Walker et al. 2019). To demarcate these zones, we used the height of the annual spring high tide from annual elevation data. Utilizing Light Detection and Ranging (LiDAR; 1 m resolution, 2 points/m²) collected via aircraft (Axis Geospatial, Easton, MD, USA), we created a digital elevation model (DEM) of the landscape. Using the LiDAR data and the DEM, we established an oceanfront intertidal range of 0.0–1.2 m elevation based on the astronomical high water at the National Oceanic and Atmospheric Administration (NOAA) Moriches Inlet tidal station, and a bayside intertidal range of 0.0–44.5 cm based on mean high water at the NOAA Smith Point Bridge tidal station (NOAA 2017).

We measured distances of each pixel to the annual spring high tide lines using the ‘Euclidean Distance’ and ‘Path Distance’ tools in ArcGIS Pro (Esri Inc., Redlands, CA, USA). We created four variables measuring foraging access (Euclidean distance to bay high tide line, Euclidean distance to ocean high tide line, least-cost distance to ocean high tide line, and least-cost distance to bay high tide line). The least-cost distance was the shortest path to the high tide line taken entirely on dry or wet sand (i.e., not crossing water or vegetation) and is used as an indicator for routes flightless chicks can use to access foraging areas (Walker et al. 2019, Robinson et al. 2021).

Other frequently studied aspects of plover habitats include proximity to the intertidal zone (Maslo et al. 2011), which may signal flood susceptibility, and proximity to dunes (Burger 1987, Maslo et al. 2011) or vegetation (Burger 1987), which might suggest exposure to threats from terrestrial predators. We merge these aspects into backshore width, where a location with a greater width mitigates flooding risk and reduces predation risk from dunes or vegetation (i.e., the backshore barrier). We defined the backshore width of where the nest is located as the distance perpendicular from the shoreline to the nearest back-beach barrier (e.g., development, dune, water, or vegetation) and calculated the backshore width of each 10-m segment perpendicular to the shoreline using the ArcGIS Pro ‘Create Fishnet’ tool (Walker et al. 2019). Lastly, we manually classified developed areas where paved roadways, buildings, or ports were present, because these areas are more prone to have human disturbance detrimental to nest or chick survival (DeRose-Wilson et al. 2018). We also used the ‘Euclidean Distance’ tool to measure each pixel’s distance to development.

To represent available nesting habitat for a use vs availability analysis (Johnson 1980), we generated random points (>60 m apart) within dry sand pixels above the spring high tide each

year such that there were four times as many random points as nests using the 'Create Random Points' tool in ArcGIS Pro (Esri, Inc., Redlands, CA, USA).

2.5 Analytical methods

We standardized the values of habitat variables in the dataset and checked for collinearity ($r < 0.70$; Dormann et al. 2013). Vegetation was sparse between nest sites and ocean spring high tide line and Euclidean distance to ocean and least-cost distance were highly correlated ($r = 0.72$). We retained least-cost distance to ocean as it accounts for barriers affecting chick navigation (Walker et al. 2019), and removed Euclidean distance to ocean from future analyses. We incorporated all uncorrelated variables in a generalized linear model with a binomial error distribution and logit link (logistic regression, R package 'lme4'; Bates et al. 2015) to assess how each variable influenced nest site selection in each year. We checked model assumptions and examined model fit with a Hosmer and Lemeshow goodness-of-fit test (Hosmer and Lemeshow 1989). We identified informative interactions where selection differed from the reference year based on whether the 95% confidence intervals overlapped zero. All analyses were performed using R ver. 4.1.1 (R Core Team 2022).

2.6 Suitability map development

We mapped suitable nesting habitat distribution during 2010 (pre-hurricane), 2015 (post-stabilization), and 2020 (post-succession). We utilized ArcGIS Pro's 'Raster Calculator' to generate maps displaying suitable nesting habitat areas based on intercepts and beta coefficients from the generalized linear model, and used the standardized raster layers of habitat variables for each year. This process involved incorporating specific year values for six variables, creating annual raster layers indicating the likelihood of plover nesting suitability ranging from 0 (low) to

1 (high) for individual dry sand pixels on the landscape. We chose a suitability threshold of 0.20 based on optimizing values of prevalence-dependent thresholds that are informed by the number of nests and random points used in the analysis (Jiménez-Valverde and Lobo 2007); all dry sand pixels were classified as suitable ($P \geq 0.20$) or unsuitable ($P < 0.20$). For each year, we quantified the proportion of suitable and unsuitable habitat based on the total evaluated area and mapped the classified layers on aerial imagery.

3. Results

We recorded 402 plover nest locations and 1,608 random points from surveys in 2010, 2015–2020 (Table 1).

3.1 Vegetation cover

Vegetation coverage in the study area during the breeding season immediately after Hurricane Sandy was 10.5% (Table 2). Following island stabilization, beach renourishment, and restoration area creation completed by early 2015, vegetation cover was reduced to 8.4%, and median vegetation cover at nests was 0.1% (IQR = 1.0%; Table 2). However, the amount of vegetation increased by 11.5% over five years of natural succession (2015–2020; Table 2). In 2020, vegetation cover was 20.0% and median vegetation cover at nests was 6.2% (IQR = 19.2%; Table 2).

3.2 Nest site selection

Values of the six variables at nests and random points fluctuated relative to the storm occurrence (Fig. 2A-F). These values informed our generalized linear regression, which fit the data well ($\chi^2 = 4.14$, $df = 8$, $p = 0.84$; Hosmer and Lemeshow 1989). After Hurricane Sandy,

plovers exhibited selection similar to pre-hurricane behavior for many of the habitat variables we evaluated. However, in 2015, plovers selected nests farther from development than in 2010 (Table 3), and in 2016, 2018, and 2020, plovers selected nests with less Euclidean distance to bay than in 2010 (Table 3).

3.3 Suitable nesting area

Pre-hurricane (2010) suitable habitat was sparsely dispersed within the eastern region of the island (Fig. 3) and concentrated within the erosive ends of the island and the narrower strip encompassing the Old Inlet area (although not formed yet; Fig. 4, 5). Post-storm and restoration area creation (2015), the majority of suitable area was concentrated around Old Inlet (Fig. 4) and distant regions of Smith Point County Park, particularly within the Great Gun restoration area (Fig. 3). Prior to the hurricane, 35.3 ha (29.8%) of the study area was suitable nesting habitat (Table 4, Fig. 3-5). Immediately post-stabilization in 2015, there was 124.3 ha (50.8%) of suitable habitat across the study area (Table 4, Fig. 3-5), largely due to the creation of the Great Gun restoration area (25.1 ha; Fig. 3). In 2020, after five years of succession, the amount of suitable habitat decreased to 102.4 ha (36.8%; Table 4, Fig. 3, 4, 5). Further, 29 of the 49 (59.1%) nests in 2010 were in suitable habitat, 32 of the 36 (88.9%) nests in 2015 were recorded in suitable habitat, and in 2020, only 36 of the 74 (49.6%) nests were recorded in areas identified as suitable (Fig. 3, 4, 5).

4. Discussion

Even though vegetation initially decreased, it swiftly reappeared in several areas on the island affected by the hurricane, and the acquisition of fine scale imagery allowed us to monitor land cover change at specified scales. The evaluation of land cover changes using remote sensing

is becoming more frequent with improved technologies (Lucas and Carter 2013, Carter et al. 2018, Velasquez-Montoya et al. 2021). Lucas and Carter (2013) and Carter et al. (2018) used satellite imagery to investigate the recovery of vegetation on Gulf of Mexico beaches after Hurricane Katrina. The gradual increase in vegetation cover in this study was consistent with the sequence and pattern displayed in the zonation of dune vegetation in Florida coastal systems, where different plant species colonized the dunes in temporal stages (Johnson 1997).

Vegetation patterns vary within dune habitats (i.e., foredunes, interdunes, and backdunes; Miller et al. 2009), and development of vegetation on dunes can be limited by water, nutrients, and disturbance (Houle 2008, Lane et al. 2008). On Fire Island, vegetation typically was denser in the island interior, and it grew rapidly in the overwash areas in Smith Point County Park (Appendix Fig. B1). Our findings are supported by another study which geographically and temporally overlapped with ours and found that vegetation density increased annually within the interdune zone. on Fire Island (Bellman 2018).

Plovers typically avoid vegetated areas for nest sites and select open, sparsely vegetated areas (Cairns 1982, Swaisgood et al. 2018, Zeigler et al. 2021, Dorsey et al. *in prep*). However, vegetation at nest sites increased with time in our study, which could indicate that there were fewer options for adult plovers to establish territories in unvegetated habitat as vegetative succession progressed. Similarly, Cohen (2008) discovered that plover nests in Westhampton Island occurred more frequently in vegetation than expected based on its availability. This observation, made approximately twelve years after a nor'easter in 1992, implies that the landscape might have undergone advanced ecological succession if also left undisturbed, and that establishing nest sites without any vegetation was unachievable by plovers or that extraneous factors, such as human disturbance level, limited nesting options in unvegetated

habitats. Increases in preferred habitat features can shift shorebird nest locations and improve productivity (Robinson et al. 2019, Walker et al. 2019). Thus, when access to important habitat features, such as foraging areas, is fragmented by physical barriers like vegetation or water polders, plovers may respond by nesting in a way that elevates their individual, nest, or chick survival.

The Fire Island plovers' preference for different habitat features largely remained consistent before and after the hurricane, with two exceptions. Selection to be farther from developed areas than expected at random is consistent with plover behavioral observations made by Wilcox (1959) and Robinson et al. (2021). Plovers also nested closer to the bayside habitats following Hurricane Sandy (Walker et al. 2019). Bayside intertidal zones are frequently linked with increased availability of invertebrate prey and serve a crucial role in nourishing offspring for migration (Loefering and Fraser 1995*b*, Elias et al. 2000, Cohen and Fraser 2010). This nest placement is also beneficial during the nesting stage because a nest is at lower risk of flooding on the lower energy bayside habitat (Burger 1987, Espie et al. 1996). Nesting on the high-energy oceanside habitat results in increasing risk of sea level rise and heightened flooding risk (Seavey et al. 2011).

Modeling suitable habitat for shorebirds allows prediction of how the habitats may shift following landscape changes (Schaffer-Smith et al. 2018, Conlisk et al. 2022). There was an increase of nests recorded in regions with suitable habitat from 2010 to 2015, consistent with behavioral observations of shorebirds increasing occupation of likely suitable storm-created habitats a few years after its initial creation rather than immediately (Maslo et al. 2019). Later, after years without disturbance (2020), the Great Gun restoration area remained a concentration of suitable habitat. The persistence in suitability of this restoration area was likely the result of

excavating extensively to access plant roots during creation, lowering potential vegetation re-establishment in the region.

The Fire Island plover population increased 173% within the study area between 2013 and 2020 in conjunction with the decrease of unvegetated areas and fluctuations in suitable nesting habitat areas, which likely led to competition for suitable nest sites (Fretwell and Lucas 1969, Village 1983). More competition for territories in a heterogeneous landscape can lead to nesting in less favorable habitats (i.e., site dependence; Rodenhouse et al. 1997). Returning to the same nesting location despite worsening habitat conditions, may indicate plovers are site dependent (Friedrich et al. 2015). Numerous shorebirds, such as plovers, depend on dynamic, young ecosystems sustained by natural occurrences like overwash or flooding events (Schupp et al. 2013, Fraser and Catlin 2019, Zeigler et al. 2019). Without these disruptions, the natural succession continues, resulting in a decline of appropriate beach nesting areas for shorebirds.

5. Conclusion

Barrier island systems are constantly changing with the wind, waves, and tides (Davis, Jr. and Fitzgerald 2009, Feagin et al. 2015). During periods of minimal disturbance in the landscape, ecological succession takes place, leading to a reduction in nesting habitat for species that rely on early-successional habitats (Zeigler et al. 2019). Given the substantial conservation efforts dedicated to them, plovers may act as an “umbrella species” for avian conservation in coastal ecosystems, as protections for plovers benefit many other shorebirds (Monk et al. 2020). Here, vegetation succession altered the nesting landscape, but plover nest site selection for several habitat features remained the same, with the exception of selecting nests further from development and close to the bayside intertidal zone in later years of succession. However, shorebird responses vary after a storm (Maslo et al. 2019, Walker et al. 2019), and across

geography (Zeigler et al. 2021). Although we documented a decline in suitable nesting habitat by the end of our study period, the study area still supports a growing plover population (Robinson et al. 2020) which prompts the question of whether rate of this growth is slowing as carrying capacity is approached. As an environment undergoes changes, an individual may respond in a way that is advantageous to the new conditions and not retain their traditional behavior (Eggers et al. 2006, Masero et al. 2007, Ellis et al. 2022) or, the advantages of site fidelity might surpass the choice of moving to a more favorable environment.

CRediT statement

Sharon S. Dorsey: Writing – Original Draft, Investigation, Formal analysis, Visualization, Writing – Review & Editing. **Katie W. Oliver:** Data Curation, Investigation. **Shannon J. Ritter:** Methodology, Formal analysis, Visualization. **Christy N. Wails:** Data Curation, Formal analysis, Writing – Review & Editing. **Samantha G. Robinson:** Data Curation, Investigation, Formal analysis, Writing – Review & Editing, Supervision. **Henrietta A. Bellman:** Data Curation, Investigation. **Sarah M. Karpanty:** Project administration, Writing – Review & Editing, Supervision. **Daniel H. Catlin:** Project administration, Writing – Review & Editing, Supervision. **James D. Fraser:** Conceptualization, Project administration, Funding acquisition, Writing – Review & Editing, Supervision.

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Tables

Table 1. Calendar year and number of nests recorded, and random points generated within Fire Island, New York 2010, 2015–2020.

Year	Nests	Random Points
2010	49	196
2015	36	144
2016	37	148
2017	51	204
2018	63	252
2019	92	368
2020	74	296

Table 2. Year since storm, sum of classified vegetation cover (%) in study area 2013–2020, and median value of classified vegetation cover and interquartile range (IQR) within 30-m of nests and random points 2015–2020 on Fire Island, New York.

Year Since Storm ^a	Classified Vegetation in Study Area (%)	Median (IQR) Classified Vegetation at Nests (%)	Median (IQR) Classified Vegetation at Random Points (%)
1	10.52	–	–
2	12.04	–	–
3	8.42	0.13 (1.04)	2.13 (17.29)
4	11.75	1.70 (4.14)	4.08 (16.39)
5	14.26	1.92 (10.17)	1.86 (17.15)
6	17.04	2.68 (13.76)	10.6 (33.18)
7	20.60	6.90 (17.15)	7.98 (26.32)
8	20.04	6.23 (19.20)	7.05 (32.87)

^a Hurricane Sandy occurred in 2012

Table 3. Standardized estimates (β), standard errors (SE), and lower and upper confidence intervals (LCL, UCL) for covariates for the generalized linear regression model comparing nest sites selected by piping plovers to random points pre-Hurricane Sandy (2010) relative to selection in years post-Hurricane Sandy (2015–2020) Fire Island, New York.

Variable	Interaction Effect	β	SE	LCL	UCL	
(Intercept) ^a		-1.159	0.223	-1.612	-0.734	*
2015		-0.978	0.452	-2.053	-0.185	*
2016		-0.631	0.344	-1.334	0.028	
2017		-0.658	0.312	-1.282	-0.051	*
2018		-0.385	0.280	-0.932	0.169	
2019		-0.585	0.270	-1.112	-0.047	*
2020		-0.348	0.267	-0.867	0.184	
Backshore width		0.717	0.269	0.195	1.256	*
Distance to development		0.289	0.637	-0.328	0.473	
Elevation		-0.396	0.216	-0.845	0.001	
Euclidean distance to bay		0.201	0.091	0.021	0.380	*
Least-cost distance to bay		-0.093	0.171	-0.446	0.230	
Least-cost distance to ocean		0.006	0.336	-0.763	0.601	
2015 × ^b	Backshore width	-0.514	0.317	-1.142	0.104	
	Distance to Development	0.635	0.292	0.075	1.224	*
	Elevation	0.131	0.350	-0.577	0.804	
	Euclidean distance to bay	0.008	0.339	-0.662	0.695	
	Least-cost distance to bay	-0.877	0.607	-2.424	0.087	
	Least-cost distance to ocean	0.069	0.424	-0.751	0.965	
2016 ×	Backshore width	-0.391	0.325	-1.034	0.244	
	Distance to development	-0.182	0.285	-0.740	0.383	
	Elevation	0.082	0.317	-0.543	0.705	
	Euclidean distance to bay	-0.673	0.304	-1.303	-0.100	*
	Least-cost distance to bay	-0.382	0.377	-1.230	0.295	
	Least-cost distance to ocean	-0.140	0.544	-1.236	0.952	
2017 ×	Backshore width	-0.345	0.315	-0.970	0.270	
	Distance to development	0.247	0.259	-0.251	0.772	
	Elevation	0.048	0.322	-0.591	0.676	
	Euclidean distance to bay	-0.449	0.248	-0.958	0.020	
	Least-cost distance to bay	-0.401	0.327	-1.084	0.212	
	Least-cost distance to ocean	-0.519	0.466	-1.482	0.422	

2018 ×	Backshore width	-0.326	0.305	-0.932	0.268	
	Distance to development	-0.026	0.2554	-0.519	0.489	
	Elevation	0.184	0.279	-0.357	0.742	
	Euclidean distance to bay	-0.488	0.234	-0.968	-0.045	*
	Least-cost distance to bay	-0.405	0.301	-1.022	0.169	
	Least-cost distance to ocean	-0.133	0.350	-0.763	0.657	
2019 ×	Backshore width	-0.175	0.293	-0.757	0.396	
	Distance to development	0.431	0.242	-0.033	0.922	
	Elevation	0.154	0.276	-0.377	0.706	
	Euclidean distance to bay	-0.266	0.180	-0.630	0.078	
	Least-cost distance to bay	-0.224	0.240	-0.699	0.249	
	Least-cost distance to ocean	-0.467	0.410	-1.268	0.400	
2020 ×	Backshore width	-0.443	0.307	-1.054	0.154	
	Distance to development	-0.115	0.245	-0.589	0.380	
	Elevation	0.048	0.280	-0.494	0.607	
	Euclidean distance to bay	-0.669	0.218	-1.119	-0.260	*
	Least-cost distance to bay	-0.164	0.257	-0.679	0.336	
	Least-cost distance to ocean	-0.386	0.397	-1.140	0.467	

^a 2010 intercept

^b The × indicates an interaction with main effect

^c The * indicates a significant effect; for an interaction term this suggests selection was significantly different than 2010 selection for a given covariate

Table 4. Dry sand (ha) and suitable piping plover habitat (ha, %) within the study area on Fire Island, New York, during focal periods in 2010, 2015, and 2020. Suitable habitat was determined from logistic regression comparing nest sites with randomly selected dry sand sites 2010, 2015–2020.

Year	Period	Dry sand (ha)	Suitable area (ha)	Suitable area (%)
2010	Pre-storm	118.30	35.32	29.86
2015	Post-stabilization	244.66	124.27	50.78
2020	Post-5 years of succession	277.95	102.39	36.84

Figures

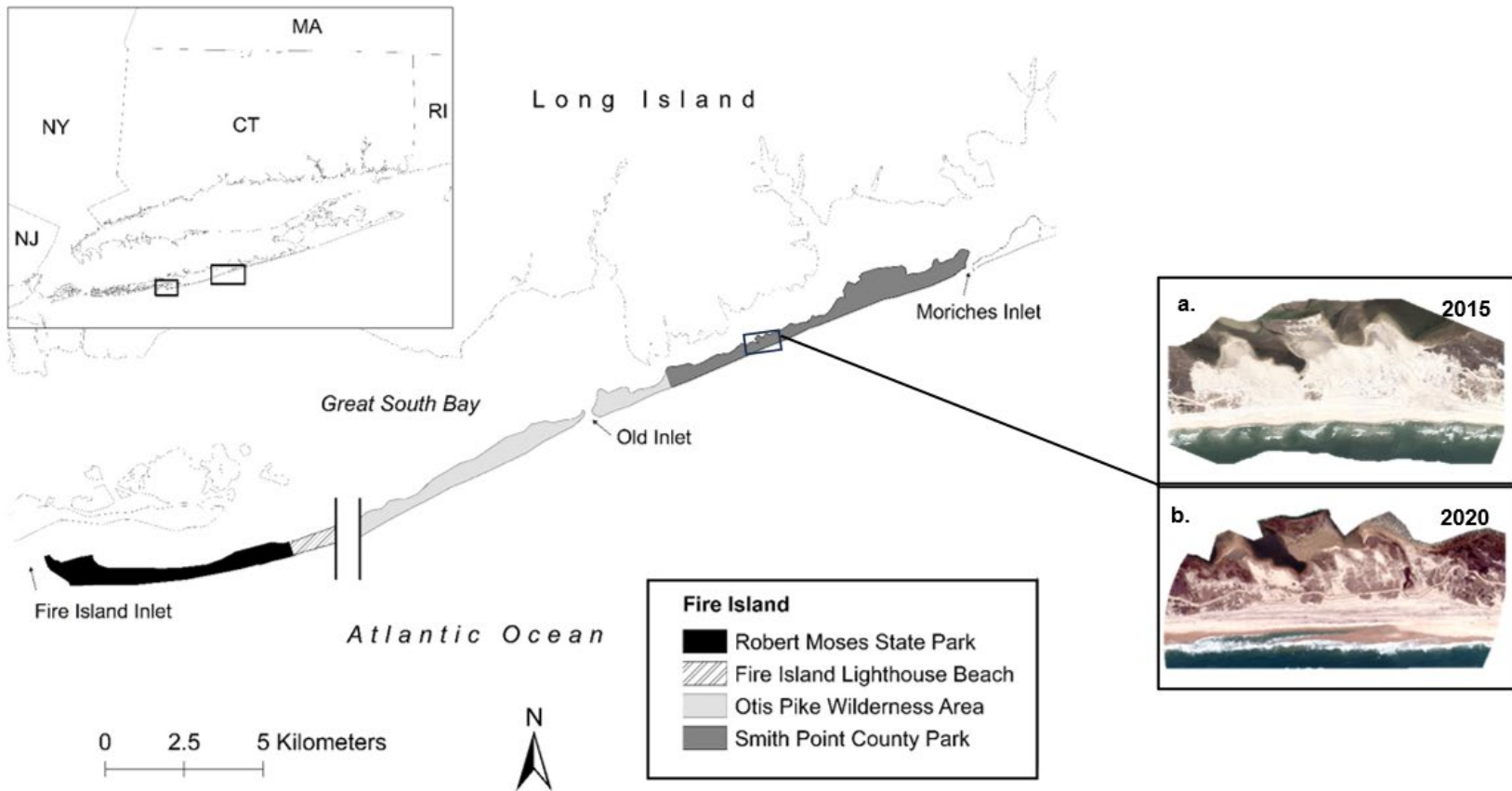


Figure 1. Map of parks within Fire Island, New York. Robert Moses State Park, Fire Island Lighthouse Beach, Otis Pike Wilderness Area, and Smith Point County Park (from left to right) comprise the study area. The area between the vertical black lines comprise a 25-km long developed area excluded from the study. Photos are from a region in Smith Point County Park where vegetation coverage increased from (a) 9.9% in 2015 to (b) 33.0% in 2020.

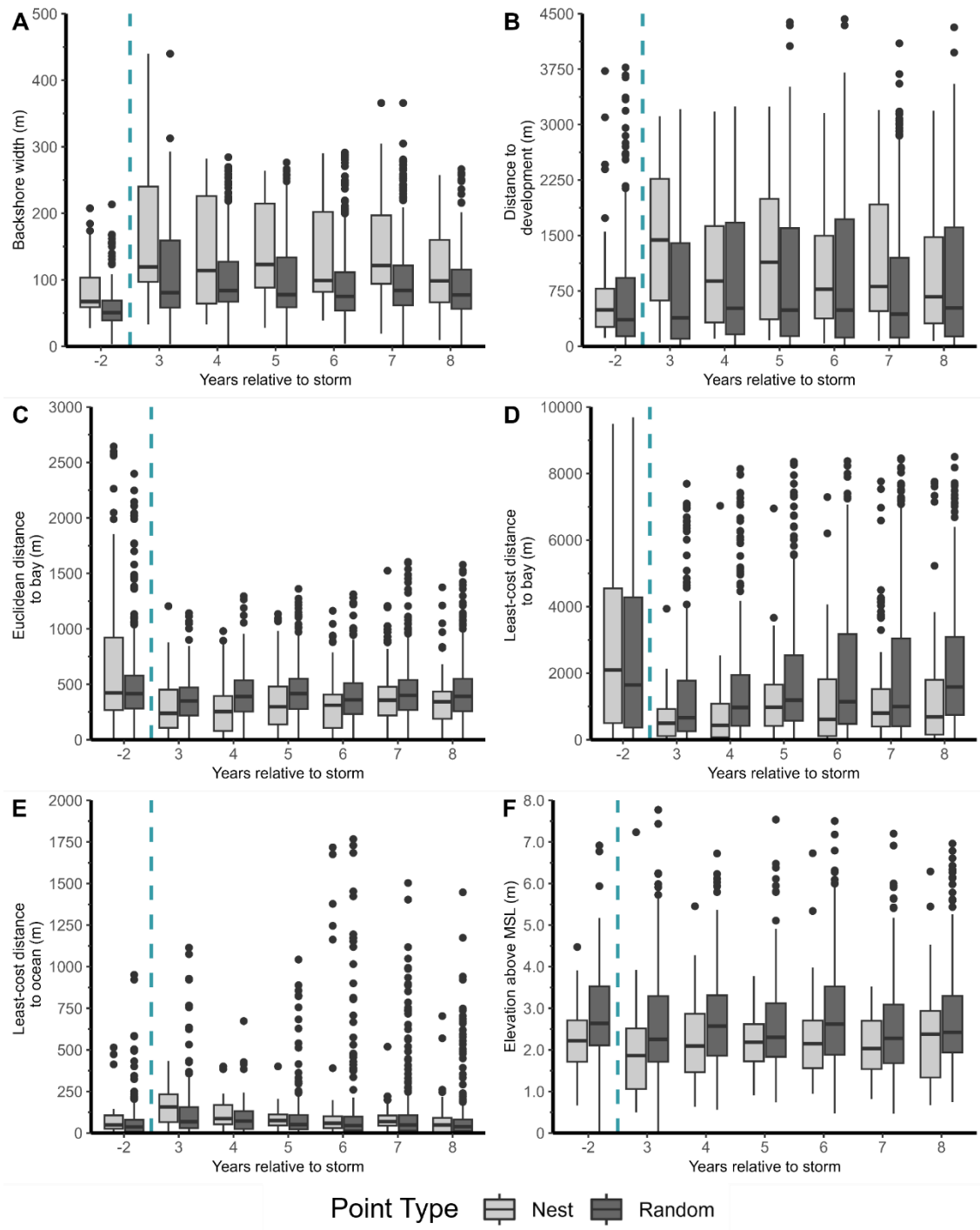


Figure 2. Boxplots for the habitat variables – (a) backshore width, (b) distance to development, (c) Euclidean distance to bay, (d) least-cost distance to bay, (e) least-cost distance to ocean, and (f) elevation – used in the logistic regression to investigate annual piping plover nest-site selection on Fire Island, New York in the years before and after Hurricane Sandy (dashed line). Values for nest sites (light gray) and at random points (dark gray) are distinguished by color. Boxplots in this figure illustrate the median as the central horizontal line within the box and the first and third quartile as the extents of the colored box. The maximum and minimum are illustrated by lines extending out from the interquartile range. Outliers are the black dots.

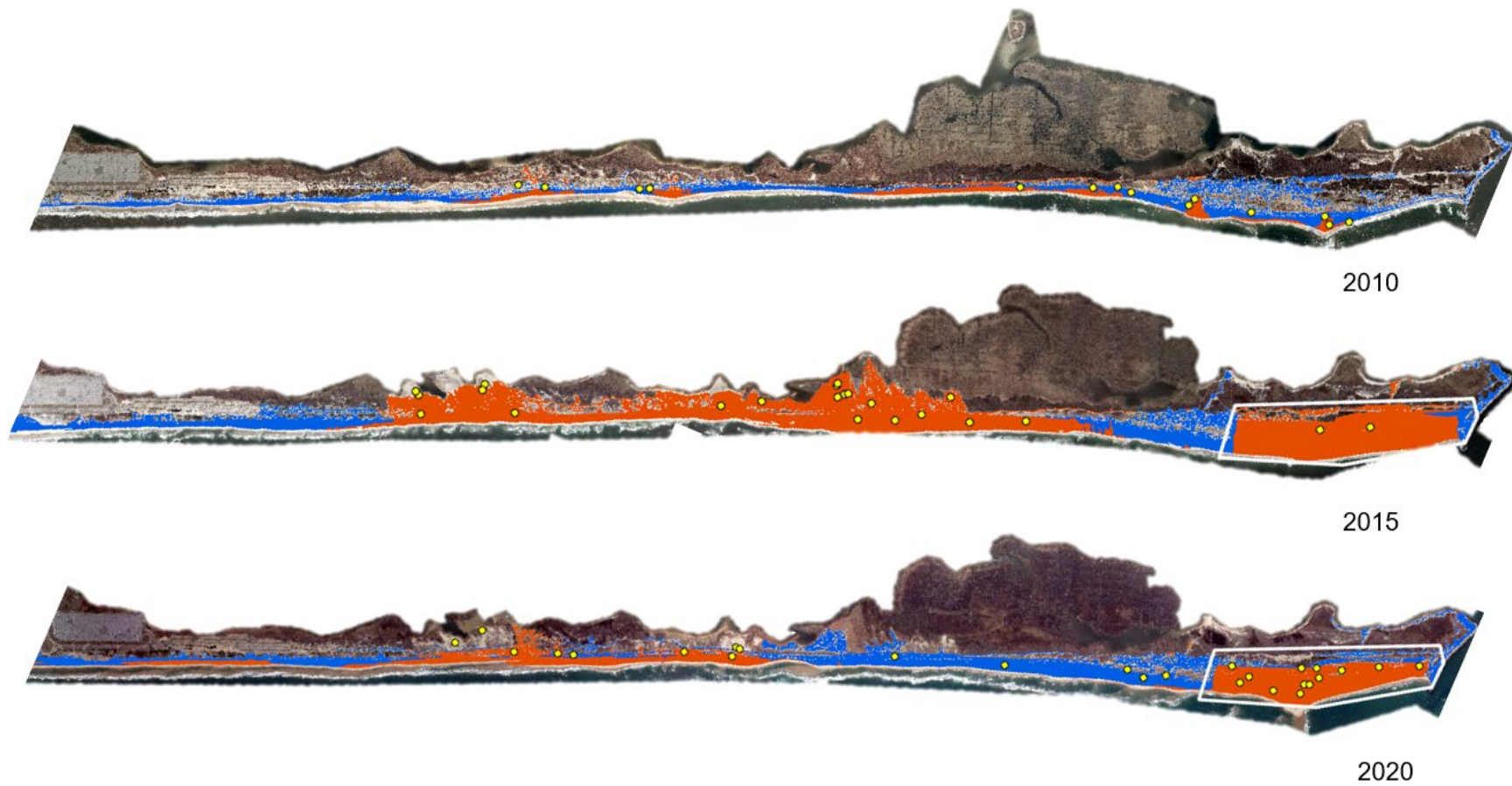


Figure 3. Suitable (red) and unsuitable (blue) piping plover nesting habitat within Smith Point County Park on Fire Island, New York, prior to Hurricane Sandy (2010), post-stabilization (2015) and following years of natural succession (2020) based on logistic regression modeling of nest-site selection. Areas classified as dry sand above the spring high tide line were modeled for suitability. The Great Gun restoration area (white outline) was present since the 2015 breeding season. Nests are shown as yellow dots.

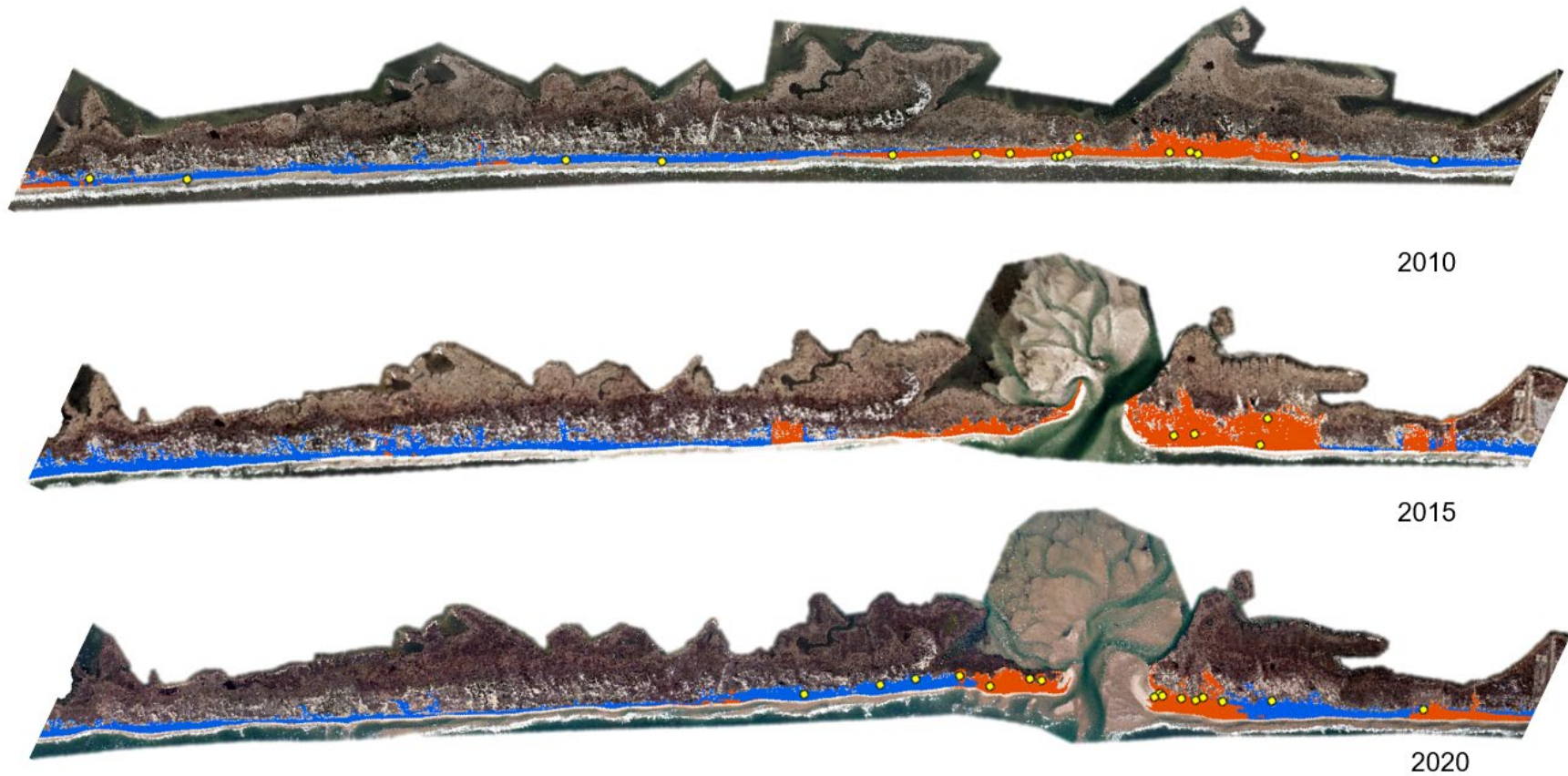


Figure 4. Suitable (red) and unsuitable (blue) piping plover nesting habitat within Otis Pike Wilderness Area on Fire Island, New York, prior to Hurricane Sandy (2010), post-stabilization (2015) and following years of natural succession (2020) based on logistic regression modeling of nest-site selection. Areas classified as dry sand above the spring high tide line were modeled for suitability. Nests are shown as yellow dots.

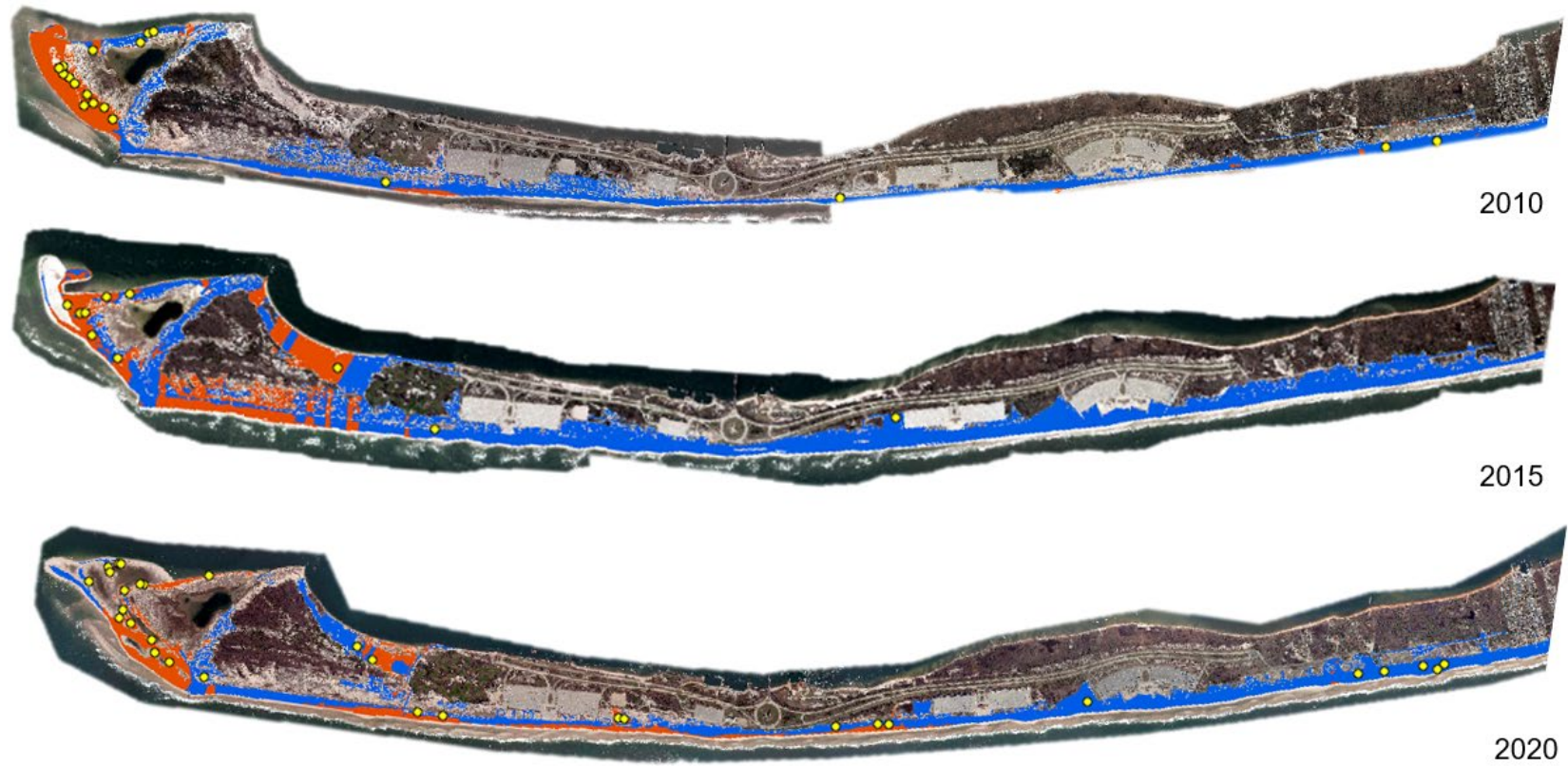


Figure 5. Suitable (red) and unsuitable (blue) piping plover nesting habitat within Robert Moses State Park and Fire Island Lighthouse Beach on Fire Island, New York, prior to Hurricane Sandy (2010), post-stabilization (2015) and following years of natural succession (2020) based on logistic regression modeling of nest-site selection. Areas classified as dry sand above the spring high tide line were modeled for suitability. Nests are shown as yellow dots.

Appendix A. Additional suitable habitat assessments for parks

Table A1. Dry sand (ha) and suitable piping plover habitat (ha, %) within each park (a. – c.) on Fire Island, New York during focal periods in 2010, 2015, and 2020. Suitable habitat was determined from logistic regression comparing used nest sites with randomly selected dry sand sites in each year.

Year	Period	Dry sand (ha)	Suitable area (ha)	Suitable area (%)
a. Smith Point County Park				
2010	Pre-storm	37.91	9.32	24.58
2015	Post-stabilization	100.12	77.12	70.03
2020	Post-5 years of succession	116.07	54.39	46.86
b. Fire Island National Seashore's Otis Pike Wilderness Area (<i>excluding Lighthouse Beach</i>)				
2010	Pre-storm	35.98	15.84	44.02
2015	Post-stabilization	51.56	25.48	49.42
2020	Post-5 years of succession	64.94	22.95	35.34
c. Robert Moses State Park (<i>including Lighthouse Beach</i>)				
2010	Pre-storm	44.42	10.15	22.85
2015	Post-stabilization	92.98	21.67	23.31
2020	Post-5 years of succession	96.94	25.05	25.84

Appendix B. Maps of annual Fire Island vegetation cover in Smith Point County Park, 2013–2020

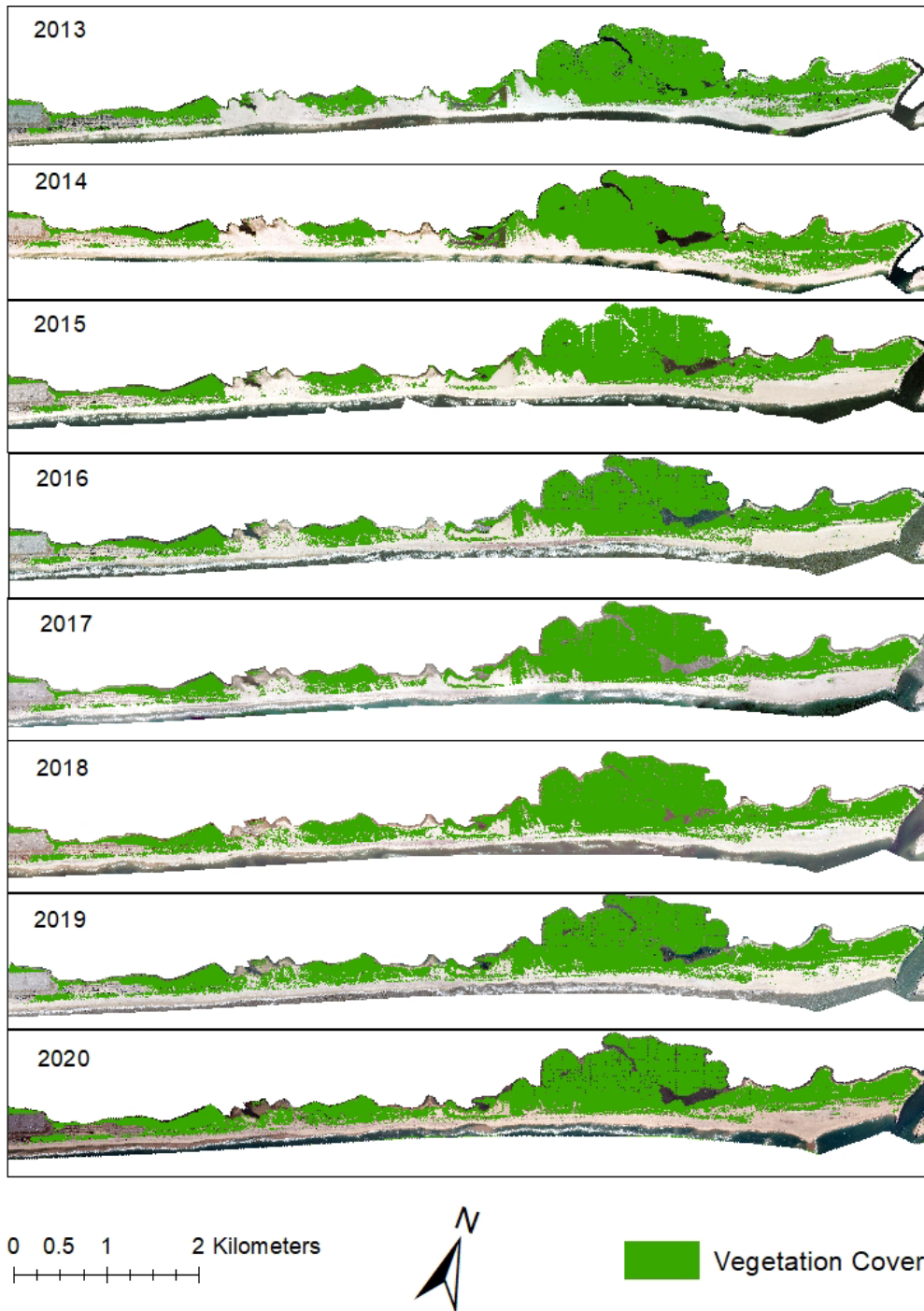


Figure B1. Classified vegetation cover (green) overlaid on annual aerial imagery in Smith Point County Park, Fire Island, New York 2013–2020 shows gradual vegetation cover change over time.

**CHAPTER 2: HEAD ON A SWIVEL: THE IMPORTANCE OF VIEWSHED IN NEST
SITE SELECTION OF A GROUND NESTING BIRD**

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Head on a swivel: The importance of viewshed in nest site selection of a ground nesting shorebird

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Keywords: barrier island morphology, piping plover, predation, remote sensing, spatial ecology, visual obstruction

Abstract

Birds and their nests are vulnerable to predation during the breeding season. Many birds have evolved nest placement strategies that minimize risk such as concealing nests in vegetation, or nesting in inaccessible cavities or on cliffs. Some ground-nesting species choose open areas where vegetative concealment or physical protection is minimal. These species may benefit from the ability to visually detect predators approaching the nest, allowing them more time to perform evasive or distracting behaviors. We studied the nesting behavior of piping plovers (*Charadrius melodus*) on Fire Island, New York from 2015–2020 to determine if the area visible from the nest (i.e., viewshed), affected nest site selection. Using a geospatial program, we calculated viewsheds at nests and random points and evaluated nest site selection using logistic regression modelling. Piping plovers selected nest sites with a greater view of predators than would be expected if nest site selection was random relative to viewshed. Viewshed to see larger predators improved the predictive ability of a previous nest site selection model that was based on habitat characteristics present on the landscape in 2015 but its influence in selection weakened as the study area underwent ecological succession. Topographic variation was the predominant visual obstruction source at plover nest sites compared to vegetation height. Viewshed may play a role

in nest site selection in other ground nesting birds, and thus is an important factor to consider in the development of habitat management strategies.

1. Introduction

The nesting period is a vulnerable stage of a bird's life (Ricklefs 1969); predators may attack nests while unattended or may be attracted to nests when parents go to and from the nest. The nesting stage often has a greater chance of failure than the hatchling, fledgling, or adult stages (Ricklefs 1969, Martin 1995, Menezes and Marini 2017, Fulton 2019). To reproduce successfully, a bird and its offspring must survive the nesting period by avoiding potential threats such as those posed by the environment (e.g., inclement weather; Habib and Davidar 2017, Terhune II et al. 2019, White Rose and Boughton 2022) or other species (e.g., predators; Sanders and Maloney 2002, Schüttler et al. 2009, DeGregorio et al. 2016). Significant nest and chick mortality can affect a species' breeding season population size (Newton 1998).

Consequently, birds have evolved adaptations to protect their nests and themselves during the nesting period (Collias 1964, Fang et al. 2018). Some nest defense behaviors are similarly deployed by birds with different nesting strategies. For example, direct physical aggression (i.e., hovering, diving, or striking) is observed in arboreal-nesting hummingbirds, ground-nesting terns, and cavity-nesting swallows (Stiles 1982, Burger and Gochfeld 1988, Lipshutz and Rosvall 2021), and indirect displays or vocalizations directed at a threat are observed in cavity-nesting woodpeckers, canopy-nesting warblers, and ground-nesting shorebirds (Short 1982, Kleindorfer et al. 2005, Gómez-Serrano and López-López 2017). Additionally, injury feigning, also called a 'broken wing display,' has been recorded in numerous species comprising 52 bird families with varying nest types and is deployed as defense against a variety of predators (de

Framond et al. 2022). Other nest protections are a function of the nesting location itself (e.g., ground, elevated, and cavity). Nesting in arboreal cavities or subterranean burrows provides protection from weather events (e.g., storms and wind) and moderates temperature fluctuations (Collias 1997). Additionally, cavity nests may be less vulnerable to predators than surface nests (Martin and Li 1992). Nesting within vegetated canopies can provide shelter and reduce detection by predators (Martin 1992, Zanette and Jenkins 2000). Surface ground nesters, however, often rely on crypsis to avoid detection and behavioral cues from other animals to initiate predator deterrence to improve survival for themselves and their eggs or young (Troscianko et al. 2016).

Many ground-nesting birds choose exposed sites in open sand, gravel, rocks, or short grass. Examples include shorebirds (Charadriiformes; Isaksson et al. 2007, Colwell 2010), passerines (Passeriformes; Minias and Janiszewski 2023), and waterfowl (Anseriformes; Laurila 1988). Cryptic coloration, stealthy nest visits, and distraction displays that lure predators away from nests or chicks may improve fitness of ground-nesting species (Mainwaring et al. 2014, de Framond et al. 2022). These strategies may compensate for the danger of nesting in the open and constitute a trade-off between selecting a suitable microclimate and minimizing predation risk (Mainwaring et al. 2014). Nesting in exposed areas is common among shorebirds, and many nest on river, bay, or ocean shorelines. Shorelines are thin areas between land and water and often are open due to occasional flooding or overwashing (the flow of water and sediment over a beach; Morton and Jr. 2003, Donnelly et al. 2006) are therefore may be especially attractive to shorebirds.

An open view of the surroundings may be important to a bird's nest site, as it could allow the bird on the nest to see an approaching predator in time to conduct its inconspicuous nest

departure and distraction display (Götmark et al. 1995, Gómez-Serrano and López-López 2014, de Framond et al. 2022). Natural and anthropogenic landscape modifications can affect a ground-nesting bird's viewshed (visible area from a specified location; Aben et al. 2018). Viewshed likely is an important component of habitat selection and level of vigilance in animals (Metcalf 1984, Aben et al. 2018). Although Gómez-Serrano and López-López (2014) showed that nest sites of Kentish plovers (*Charadrius alexandrius*) had greater viewsheds than control points, viewshed has not yet been formally tested as a factor in nest site selection models for any other ground-nesting species, due in part, to the difficulty of estimating it in a field setting (Burger 1987, Yanes et al. 1996, Gómez-Serrano and López-López 2014, Swaisgood et al. 2018). However, applications of remote sensing have been explored as a new approach to measure viewshed in wildlife habitats (Camp et al. 1997, Aben et al. 2018).

The piping plover (*Charadrius melodus*; hereafter 'plover') is an imperiled shorebird (USFWS 1985, SARA 2002) that nests on sandy beach and sandbar habitats in North America.

Obstruction of viewshed by vegetation has been suggested as a factor in plover nest site selection (Burger 1987, Cohen et al. 2008, Swaisgood et al. 2018). We investigated the hypothesis that plovers select nest sites with relatively open viewsheds by quantifying the change in viewshed over time with vegetative growth and topographic changes using remote sensing technology. Our objectives were to (1) test whether viewshed was greater at nests than at random points (2) determine if adding viewshed as a covariate improves the predictive ability of a previous model of nest site selection (Walker et al. 2019), (3) determine if the effects of viewshed changed through the course of ecological succession following Hurricane Sandy, and (4) characterize the relative importance of vegetation and topography in obstructing the viewshed at plover nests

across the study period by comparing the amount of visible area at nest sites with the effect of each obstruction source isolated.

2. Methods

2.1 Study species

The plover is a small, sand-colored, ground-nesting migratory shorebird inhabiting coastal, lacustrine, and riverine shorelines in the United States and Canada (Elliott-Smith and Haig 2020). Between mid-March and May, individuals within the Atlantic Coast population return from the south to northern breeding grounds stretching from North Carolina, USA to Newfoundland, Canada and begin establishing pairs (Elliott-Smith and Haig 2020). Males begin courting females shortly after their arrival by nest-scraping; egg-laying and incubation follow shortly thereafter (Elliott-Smith and Haig 2020). Both sexes incubate the clutch (typically four eggs), for 26–30 days until the precocial chicks hatch (Wilcox 1939). The overall nesting period (i.e., at least one pair still incubating) spans from early-April to late-July (Wilcox 1939, Cohen et al. 2009). Plovers typically nest on open sand or gravel, where the bird's sandy plumage and disruptive coloration provides cryptic protection from detection. When a predator is seen during the incubation period, parental plovers may perform several anti-predator behaviors including a stealthy nest departure, feigning injury, false brooding away from the nest, and vocal distractions to lure predators away from their nest (Cairns 1982, Fraser and Catlin 2019).

2.2 Study area

We studied plovers on Fire Island, New York (40.710604°N, -72.931583°W; Fig. 1). Fire Island is a narrow barrier island near the south shore of Long Island. Main habitats included ocean-front sandy beaches, bayside intertidal flats, undulating dune systems, sparse forests, and marshlands

(Walker et al. 2019, Robinson et al. 2021). Such coastal systems are dynamic, and frequent storms drive changes in vegetation coverage and island geomorphology (Schroeder et al. 1979, Feagin et al. 2015a). In October 2012, Hurricane Sandy, a storm system 1,770 km in diameter, hit the coast of several New York and New Jersey barrier islands (Halverson and Rabenhorst 2013). The hurricane breached the island reopening Old Inlet; Fig. 1. The island is bounded by the Atlantic Ocean to the south, Fire Island Inlet to the west, the Great South Bay and several smaller bays to the north, and Moriches inlet to the east (Fig. 1). Following Hurricane Sandy, from 2014–2016, the U.S. Army Corps of Engineers (USACE) built dunes, widened parts of the beach, and planted American beachgrass (*Ammophila breviligulata*) to stabilize the shoreline (USACE 2014).

2.3 Terrestrial predator community

Predators in the area included red fox (*Vulpes vulpes*), northern raccoon (*Procyon lotor*), Virginia opossum (*Didelphis virginiana*) and feral cat (*Felis catus*; Black 2021, Black et al. 2023), and each is a known or likely predator of plovers or their nests (Lauro and Tanacredi 2002, Ivan and Murphy 2005, Cohen et al. 2009, Black 2021a). The red fox population within the study area was heavily monitored throughout a sarcoptic mange outbreak (2014–2017), until their extirpation in 2017 (Black 2021). Red foxes imposed an indirect threat (e.g., nest disturbance, fear), but no physical evidence of plover consumption was reported within the study area (Black 2021). Definitive adult plover consumption by a cat within the study area was documented via fecal sample in 2018 (Black 2021), and numerous plover nest failures have been attributed to depredation on the adjacent Westhampton Island (Winter and Wallace 2006).

2.4 Field methods

2.4.1 Nest searching

We surveyed beaches for plovers April to August during 2015–2020. We searched for plover nests every 1–3 days by walking transects within potential dry-sand nesting habitat and by observing piping plover behavior (Walker et al. 2019, Robinson et al. 2020, 2021). We recorded nest locations using a Trimble Geo7x GPS unit (Trimble, Sunnyvale, CA, USA). We visited all nests every 1 – 3 days until they hatched or failed. We used nesting data from land managers in 2020 as the COVID-19 pandemic limited our fieldwork.

2.4.2 Vegetation sampling

We used vegetation height data recorded during plover nest initiation at randomly selected points from April to June during 2016, 2017, and 2022. We used ArcMap 10.5 (2016–2017; Esri, Inc., Redlands, CA, USA) to generate random points (>60 m apart) across the study area each year. Once we navigated to the point, we placed a 1-m quadrat on the ground, and if vegetation was present, we recorded the dominant plant species (i.e., most coverage) in the quadrat. We measured the maximum vegetation height (± 0.1 m) using a Robel Pole (Robel et al. 1970, Bellman 2018). In 2022, we returned to all the same points where vegetation was recorded in 2016 or 2017 and re-sampled the vegetation within the 1-m quadrat.

2.5 Data analyses

2.5.1 Imagery classification

We obtained aerial imagery (15-cm resolution) and Light Detection and Ranging (LiDAR; 1-m resolution, 2 pt/m²) by aircraft during the nest site selection period in April 2015–2020 (Axis Geospatial LLC., Easton, MD, USA). We classified the imagery into four land cover classes (dry

sand, wet sand, water, and vegetation), using the ‘Maximum Likelihood Classification’ tool in ArcGIS 10.6 (Esri, Inc., Redlands, CA, USA). We manually interpreted human infrastructure or development (e.g., parking lots, jetties, buildings) from the imagery (Walker et al. 2019, Robinson et al. 2021, 2023). We used LiDAR (NAVD 1988) to determine the annual ground elevation across the landscape. Since the timing of aerial imagery did not consistently align with low tide, we used LiDAR data to determine intertidal zones. The ocean intertidal line was set to below 0–1.2 m above mean sea level (MSL) in elevation, calculated in reference to the highest astronomical tide at the NOAA Moriches Inlet tidal station. The bay intertidal line was set to 0.44 m above MSL, determined by mean high water measurements at the NOAA Smith Point Bridge tidal station (NOAA 2017).

2.5.2 Calculating viewshed and spatial variables

We generated random points using the ‘Create Random Points’ tool in ArcGIS Pro (Esri, Inc., Redlands, CA, USA). In each year we created 4 random points for each nest point. Points were constrained to be within pixels classified as dry sand and > 30 m away from the nearest random point. We estimated the viewshed at nests and random points in 2015–2020 using the ‘Viewshed’ tool in ArcGIS Pro. This tool classifies pixels as visible or not visible from an observation point given visual obstructions near the observation point. We calculated viewshed from the perspective of an incubating plovers’ eye height (6 cm; Elliott-Smith and Haig 2020), and for the surrounding landscape we used ground elevation and classified vegetation (15-cm resolution). To account for vegetation height, we used the sampled vegetation heights in a logarithmic regression to estimate annual median height for 2015–2020 and added those height values uniformly to ground elevation where pixels were classified as vegetation. We used the above ground level settings within the ‘Viewshed’ tool to establish viewshed conditions based on

an incubating plover's ability to see predators. The above ground level setting classifies each 15-cm pixel by whether an object \geq a specified height would be seen by the observer given the landscape features (Fig. 2a). We first examined a plover's ability to view the full suite of common terrestrial predators of various sizes in the study area (i.e., red fox, raccoon, possum, and feral cat; 'all predators viewshed'), assuming that the ability to see the smallest predator (feral cat) implies the ability to see taller predators as well. We used a cat's average shoulder height (24.4 cm; Sunquist and Sunquist 2002) as the above ground level setting when quantifying the all predators viewshed. We also examined a plover's ability to view a red fox ('large predators viewshed'), the tallest common terrestrial predator (average shoulder height 48.8 cm; Nowak 1999) and known to be a key threat to Fire Island plovers (Cohen et al. 2009, Black et al. 2023). We established the above ground level setting as 48.8 cm to quantify the large predators viewshed while predators $<$ 48.8 cm in height would likely be obscured. We restricted the viewshed analysis to a 30-m radius from each point based on the approximate flush distances (i.e., the distance between the bird and a perceived threat at which the bird leaves its nest; Cairns 1982, Burger 1987, Loegering 1992). We report the area in which it would be possible for an incubating plover to see terrestrial predators (all predators, large predators) within the buffer as a percentage of the total 30-m buffer area (approximately 2,815 m²).

Walker et al. (2019) reported six variables believed to influence plover nest site selection in 2015, after hurricane Sandy, in a study area that overlapped ours. We used ArcGIS to calculate the same variables: Euclidean distance to bay intertidal zone (m), least cost distance to bay intertidal zone (m), least cost distance to ocean intertidal zone (m), elevation (m), distance to nearest development (m), and backshore beach width (m). Euclidean distance, calculated using the 'Euclidean Distance' tool, was the shortest distance from a point to an intertidal line. Least

cost distance, calculated using the ‘Path Distance’ tool, was the shortest distance achievable by a walking plover remaining on wet or dry sand (i.e., avoiding vegetation or open water).

Backshore beach width was the distance perpendicular from the shoreline to the nearest back-beach barrier (i.e., vegetation or elevation change > 3 m) and calculated for every 10-m section of the study area using the ‘Create Fishnet’ tool. To directly compare with the methods employed in the Walker et al. (2019) study, we computed values for the same six variables for the nests and random points in 2015, but also both viewshed values.

2.5.3 Statistical analyses

We examined whether the large predators viewshed or the all predators viewshed was more predictive of nest site selection and also whether the viewshed variable made the model with the variables from Walker et al. (2019) more informative. We standardized all habitat variables in the dataset and constructed generalized linear models (GLMs) with a binomial error distribution and logit link, as our dependent variable represented ‘used’ locations and random points represented ‘available’ locations (third order selection; Johnson 1980, Hosmer and Lemeshow 1989) via the R package ‘lme4’ (Bates et al. 2015). We considered eight candidate models: 1) Walker et al. (2019) variables, 2) Walker et al. (2019) variables plus the large predators viewshed, 3) Walker et al. (2019) variables plus the all predators viewshed 4) Walker et al. (2019) variables plus the large predators viewshed and years since storm (i.e., Hurricane Sandy), 5) Walker et al. (2019) variables plus the all predators viewshed to and years since storm, 6) Walker et al. (2019) variables plus the large predators viewshed and years since storm and the interaction, 7) Walker et al. (2019) variables plus all predators viewshed and years since storm and the interaction, and 8) a null (intercept-only). We checked model assumptions, measured fit of the models with a Hosmer and Lemeshow goodness-of-fit test (Hosmer and Lemeshow 1989),

compared the eight models using Akaike's Information Criterion (AIC; Akaike 1974) corrected for sample size bias (AIC_c ; Hurvich and Tsai 1989), and selected the top-ranked model when $> \Delta 2 AIC_c$ (Burnham and Anderson 2007). The most parsimonious model (lowest AIC_c) in the comparison was chosen as the top model if there was $> \Delta 2 AIC_c$ between the first and second ranked models (Burnham and Anderson 2007). To determine the overall influence of viewshed on nest site selection, we evaluated the top-ranked additive candidate model containing a viewshed variable and compared the ΔAIC_c values of models with large predator vs. all predators viewshed. We also assessed whether viewshed retained its importance in plover nest site selection over time in the years since storm (2015–2020), a period when vegetation and topography changed from succession, by evaluating the beta coefficient of the interaction between the years since storm and the viewshed variable. All analyses were conducted in R ver. 4.1.1 (R Core Team 2022).

To determine the contribution of visual obstruction caused by topography as compared to vegetation at plover nests, we conducted another viewshed analysis in ArcGIS Pro using only the ground elevation (i.e., no vegetation height added) to show where the plover's view was obstructed by topography. We then subtracted the results of the two viewshed analyses (i.e., vegetation and topography minus topography only) to isolate each contribution of each obstruction type to a plover's obstructed viewshed. We tested the difference in means of each obstruction type using a two-sample t-test ($\alpha = 0.05$).

3. Results

3.1 Viewshed

We sampled plots for vegetation height in 2016 ($n = 16$), 2017 ($n = 30$), and 2022 ($n = 55$) to inform the inputs for the viewshed analyses. The change in median vegetation height in sampling years suggests an annual increase over time (2016: median height = 10 cm, IQR = 20 cm; 2017: median height = 20 cm, IQR = 20 cm; 2022: median height = 50 cm, IQR = 10 cm), and annual predicted vegetation heights for 2015–2020 are shown in Table 1. The ground elevation within nest buffers ranged from 0.69 m below MSL to 11.06 m above MSL.

During 2015–2020, we recorded 353 nests and generated 1412 random points in the study area. Viewshed values ranged from completely open (100%) to nearly fully obstructed (0.03%) within the 30-m buffer (Table 2). Nest site visible area was greater in the years shortly after post-Hurricane Sandy beach stabilization (i.e., 2015–2016), but it declined in later years (i.e., 2017–2020). Most (73.4%) nest sites had at least 50% visible area to see any terrestrial predators. The large predators viewshed median value of percent visible area was always greater than the all predators viewshed (Table 2). The visible area at nest sites and at random points became more similar over time.

Incorporating the viewshed variables improved the model using variables examined by Walker et al. (2019) for plover nest site selection, and all models including viewshed were ranked higher (lower $\Delta AICc$) than the models without it (Table 3). The model accounting for the interaction between large predators viewshed and years since storm was the most informative model ($\omega = 0.85$; Table 3). We determined that plovers also selected nest sites with greater large predators viewshed ($\beta = 1.26$, $SE = 0.31$, 95% $CI = 0.66 - 1.88$; Table 4) although this interpretation does not account for annual variation. As the time since hurricane sandy increased, importance of viewshed in nest site selection declined ($\beta = -0.13$; $SE = 0.05$; 95% $CI = -0.23 - -0.04$; Table 4).

3.2 Visual obstruction sources

The contribution of vegetation height and topography to visual obstruction at nests fluctuated annually (Table 5). Most (77%) of the visual obstruction within a nest site viewshed was caused by topographical (elevation) variation. Across all years of our investigation, vegetation obstructed a plover's view of larger predators marginally (median = 0.21%, IQR = 3.54%; Table 5); however, topography obstructed the view (median = 13.7%, IQR = 28.4%; Table 5) to a greater degree than vegetation height ($t = -12.64$; $df = 704$; $p < 0.001$).

4. Discussion

4.1 Viewshed's role in nest site selection

This study provided quantitative evidence that viewshed is important in plover nest site selection and provides a way to compare visibility across sites. Several bird species prefer higher visibility sites over more obstructed ones (Eason and Stamps 2001, Krams 2001) and our study agrees with this statement. Our findings of plovers selecting nest sites with greater viewshed to see predators than would be expected at random complements another study which found that an unobscured view increases the ability of ground-nesting mallards (*Anas platyrhynchos*) to detect approaching predators (Javůrková et al. 2011). Staying vigilant about the threats from predators is essential for the survival of prey species. In a meta-analysis of 53 studies of predation on bird's nests in multiple habitats in North America, 24% of nests were lost to terrestrial predators, of which 63% were canids, northern racoons, and Virginia opossums (DeGregorio et al. 2016). Similarly, it has long been asserted that plovers favor open nesting areas (Burger 1987, Prindiville Gaines and Ryan 1988, Espie et al. 1996). Burger (1987) asserted that plovers'

selection for open areas increases the potential for predator detection. Despite this, quantitative evidence about nest site selection was lacking.

The line of sight between predator and prey is a function of predator height, distance to one another, and landscape features (e.g., vegetation height and microtopography; Andersson et al. 2009). When the predator is not easily detectable, or visible, a bird is less likely to spot the predator itself (Whittingham et al. 2004), and predation risk of its nest may increase because the parent must first detect the predator before realizing the need to take evasive action (Devereux et al. 2006). This study evaluated conditions where known terrestrial predators would be within a plover's line of sight given the predators' heights and the landscape features. Although both viewshed conditions predicted nest site selection better than the null model, the large predators viewshed was a stronger indicator than the all predators viewshed, suggesting that plovers selecting nest sites that offer visibility of the furthest extent their surroundings.

Vegetation coverage increased during the study, shrinking the amount of unvegetated nesting habitat available to plovers. Additionally, the fox population was extirpated due to sarcoptic mange (Black 2021). As the predator community and land cover changed, the effect of predator viewshed on plover nest site selection seemed to decline. There are several possibilities for viewshed's shift in importance. First, plovers may be prioritizing other nest site variables (e.g., avoiding flood-prone low elevation areas) in a way that compromises the visibility at nest sites. Similarly, Oriental storks (*Ciconia boyciana*) demonstrate compromising adaptive nesting strategies by nesting further from food sources in areas of higher human disturbance, prioritizing nest protection over resources access (Cheng et al. 2023). Second, as plover population density rose in a heterogenous habitat, the competition for nests with ample visibility intensified, forcing some plovers into visually obscured nesting sites. (i.e., site dependence; Rodenhouse et al. 1997,

Weithman et al. 2019, Robinson et al. 2020). A study on shags (*Phalacrocorax aristotelis*) revealed an inverse relationship between population size and the average suitability of nest sites occupied (Potts et al. 1980). Third, the extirpation of the plover's primary predator, the red fox, could have reduced the importance of viewshed to detect fox in the succeeding years (i.e., predator-induced plasticity; Eggers et al. 2006). The decline of terrestrial predator abundance and emergence of aerial predators reliant on visual search of prey could signal a switch in the role of cover and camouflage in plover nest site selection (Swaisgood et al. 2018), where predator avoidance becomes the priority instead of predator detection.

4.2 Visual obstruction

Vegetation has been widely believed to be the primary source of limiting visibility in ground-nesting birds (Dwernychuk and Boag 1972, Cairns 1982, Prindiville Gaines and Ryan 1988, Espie et al. 1996, Lomas et al. 2014, Laidlaw et al. 2020). However, in this study, topography, not vegetation height, was the primary source of visual obstruction to an incubating plover. This finding is consistent with the widely understood belief that landscape features can impede visibility of other individuals in a shared environment (Burger 1977, Metcalfe 1984, Martin 1993, Andersson et al. 2009). This study is the first assessment of the effect of microtopography as a type of visual obstruction to ground-nesting birds, although it has previously been noted as source of obstruction in predator-prey visibility (Andersson et al. 2009). Larger topographical features, like beach dunes, are more widely accepted as view-obstructing features (Stantial et al. 2020). Beach dunes have been a variable of interest for shorebird habitat selection in terms of distance to nest (Burger 1987, DeRose-Wilson et al. 2013, Grant et al. 2019), and as an overall nesting habitat type (DeRose-Wilson et al. 2013), in addition to nest elevation (Gieder et al. 2014, Walker et al. 2019, Zeigler et al. 2021). Nesting in shallow depressions reduces predator

visibility but increases vulnerability to depredation, while elevated sites enhance visibility but risk exposure to wind-driven sand abrasion and depredation (Burger 1987).

Over the course of ecological succession, vegetated dune systems developed across the nesting habitat through a positive feedback loop between sand deposition and plant colonization (Krajnyk and Maun 1981, Maun 2009). We noted that both vegetation and topography obstruction within the nest sites increased over time suggesting that these features were more frequently within nesting sites in increasing years post-storm.

5. Conclusion

Viewshed as measured by modern techniques can provide insight into how birds select habitats. This study contributes to nascent viewshed techniques investigating animal behavior (Aben et al. 2018, Stein et al. 2022, Ucerro et al. 2023), and it is the first conducted for ground-nesting shorebird species or performed with such fine-scale geospatial layers allowing for the three-dimensional visualization. Importantly, this geospatial approach offers an innovative and consistent method for viewshed assessment in other ground-nesting species, as it can be adapted for other birds of conservation concern, such as the red knot (*Calidris canutus*), bar-tailed godwit (*Limosa lapponica*), and mountain plover (*Charadrius montanus*). Quantifying viewshed offers insight into the role of nest visibility and concealment for species' habitat selection behavior. Further investigation into overlooked factors shaping nest-site selection choices using new approaches allows for more informed and tailored conservation strategies particularly when conventional methods fall short.

CRedit statement

Sharon S. Dorsey: Writing – Original Draft, Investigation, Formal analysis, Visualization, Writing – Review & Editing. **Shannon J. Ritter:** Methodology, Formal analysis, Visualization. **Christy N. Wails:** Data Curation, Formal analysis, Writing – Review & Editing. **Samantha G. Robinson:** Data Curation, Investigation, Formal analysis, Writing – Review & Editing, Supervision. **Katie W. Oliver:** Data Curation, Investigation. **Henrietta A. Bellman:** Data Curation, Investigation. **Sarah M. Karpanty:** Project administration, Writing – Review & Editing, Supervision. **Daniel H. Catlin:** Project administration, Writing – Review & Editing, Supervision. **James D. Fraser:** Conceptualization, Project administration, Funding acquisition, Writing – Review & Editing, Supervision.

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Tables

Table 1. Annual predicted vegetation height on Fire Island, New York based on sampled plots in 2016, 2017, and 2022.

Year	Years Since Storm ^a	Vegetation Height (cm)
2015	3	15.0
2016	4	21.0
2017	5	28.0
2018	6	34.0
2019	7	40.0
2020	8	46.0

^a Hurricane Sandy occurred in 2012

Table 2. Calendar year, years since storm, sample size (n), median (%), interquartile range (IQR; %), and range (%) of visible area using the large predator viewshed (i.e., where a red fox is visible within 30-m buffer) and the all predators viewshed (i.e., where all terrestrial predators are visible within 30-m buffer) for plover nests and random points in Fire Island, New York 2015–2020.

Year	Years Since Storm ^a	n	Nests				Random Points				
			<i>Large Predator Viewshed</i>		<i>All Predators Viewshed</i>		<i>Large Predator Viewshed</i>		<i>All Predators Viewshed</i>		
			Median (IQR)	Range	Median (IQR)	Range	Median (IQR)	Range	Median (IQR)	Range	
2015	3	36	96.43 (21.23)	23.73 – 100.00	89.81 (25.70)	18.01 – 100.00	144	69.52 (48.29)	3.65 – 100.00	53.77 (49.24)	2.61 – 100.00
2016	4	37	93.48 (30.88)	38.73 – 100.00	81.72 (38.50)	25.81 – 100.00	148	69.92 (44.60)	0.77 – 100.00	55.51 (43.50)	0.36 – 100.00
2017	5	51	76.60 (30.89)	17.31 – 100.00	64.19 (35.49)	7.30 – 97.92	204	75.88 (45.80)	10.39 – 100.00	63.00 (43.11)	7.10 – 100.00
2018	6	63	81.31 (30.48)	7.01 – 100.00	69.79 (37.01)	4.51 – 100.00	252	64.91 (42.44)	0.18 – 100.00	54.04 (43.41)	0.09 – 100.00
2019	7	92	74.83 (33.36)	13.60 – 100.00	64.82 (39.49)	9.81 – 100.00	368	74.60 (45.00)	0.35 – 100.00	63.48 (48.65)	0.19 – 100.00
2020	8	74	75.49 (32.60)	0.99 – 100.00	62.41 (35.20)	0.67 – 99.99	296	63.61 (50.42)	0.06 – 100.00	50.36 (49.10)	0.03 – 100.00
All years	--	353	81.67 (32.96)	0.99 – 100.00	69.17 (39.54)	0.67-100.00	1412	68.65 (46.53)	0.06 – 100.00	57.25 (47.91)	0.03 – 100.00

^a Hurricane Sandy occurred in 2012

Table 3. Candidate generalized linear models (binomial error distribution, logit link) including previously tested variables from Walker et al. (2019), viewshed, and years since storm (i.e., Hurricane Sandy) ranked by Akaike’s information criterion corrected for small sample sizes (AIC_c) with predator class-based viewshed conditions comparing nest sites selected by piping plovers (*Charadrius melodus*) to random points in Fire Island, NY in 2015–2020.

Model ^a	k^b	ΔAIC_c	ω^c	LL ^d
Distance to bay + Distance to development + Least cost distance to bay + Least cost distance to ocean + Elevation + Backshore beach width + (Large predators viewshed × Years since storm)	10	0.00	0.85	-787.06
Distance to bay + Distance to development + Least cost distance to bay + Least cost distance to ocean + Elevation + Backshore beach width + (All predators viewshed × Years since storm)	10	4.59	0.09	-789.35
Distance to bay + Distance to development + Least cost distance to bay + Least cost distance to ocean + Elevation + Backshore beach width + Large predators viewshed + Years since storm	9	5.52	0.05	-790.83
Distance to bay + Distance to development + Least cost distance to bay + Least cost distance to ocean + Elevation + Backshore beach width + Large predators viewshed	8	8.78	0.01	-793.47
Distance to bay + Distance to development + Least cost distance to bay + Least cost distance to ocean + Elevation + Backshore beach width + All predators viewshed + Years since storm	9	12.35	0.00	-794.25
Distance to bay + Distance to development + Least cost distance to bay + Least cost distance to ocean + Elevation + Backshore beach width + All predators viewshed	8	15.13	0.00	-796.65
Distance to bay + Distance to development + Least cost distance to bay + Least cost distance to ocean + Elevation + Backshore beach width	7	37.49	0.00	-808.83
Null	1	174.18	0.00	-883.21

^a Model covariate large predators viewshed is defined as 48.8 cm above ground level; all predators viewshed is defined as 24.4 cm above ground level; Years since storm = 2015 is 3 years post-storm, etc.; Walker et al. 2019 variables include: Distance to bay, Distance to development, Least cost distance to bay, Least cost distance to ocean, Elevation, and Backshore beach width

^b Number of parameters

^c Model weight

^d Log Likelihood

Table 4. Standardized estimates (β), standard errors (SE), and lower and upper 95% CIs for covariates for the top-ranked generalized linear model (binomial error distribution, logit link) comparing nest sites selected by piping plovers (*Charadrius melodus*) to random points in Fire Island, New York in 2015 – 2020.

Covariate ^a	β	SE	Lower 95% CI	Upper 95% CI
Intercept	-2.35	0.29	-2.91	-1.77
Years since storm	0.11	0.04	0.03	0.20
Large predators viewshed	1.26	0.31	0.66	1.88
Distance to bay	-0.24	0.07	-0.39	-0.10
Distance to development	0.24	0.06	0.12	0.37
Least cost distance to bay	-0.37	0.09	-0.55	-0.21
Least cost distance to ocean	-0.16	0.08	-0.31	-0.02
Elevation	-0.14	0.08	-0.30	0.03
Backshore beach width	0.32	0.06	0.21	0.44
Years since storm \times Large predators viewshed	-0.13	0.05	-0.23	-0.04

^a Covariates are defined as: Years since storm = 2015 is 3 years post-storm, etc., and large predators viewshed = 48.8 cm above ground level

Table 5. Calendar year, years since storm (i.e., Hurricane Sandy), median area (%) and interquartile range (%) of visual obstruction of caused by vegetation or topography within the 30-m nest buffer at piping plover (*Charadrius melodus*) nests on Fire Island, NY in 2015–2020. Values are derived from the large predators viewshed (i.e., where a red fox is visible within 30-m buffer).

Year	Years Since Storm ^a	Median Vegetation Obstruction Area (IQR)	Median Topography Obstruction Area (IQR)
2015	3	0.00 (0.00)	3.52 (21.23)
2016	4	0.07 (1.63)	6.01 (17.58)
2017	5	0.73 (1.91)	19.69 (31.33)
2018	6	0.02 (2.16)	12.56 (25.75)
2019	7	1.56 (6.37)	16.57 (29.56)
2020	8	0.47 (7.01)	17.39 (25.53)
All Years	--	0.21 (3.54)	13.73 (28.41)

^a Hurricane Sandy occurred in 2012

Figures

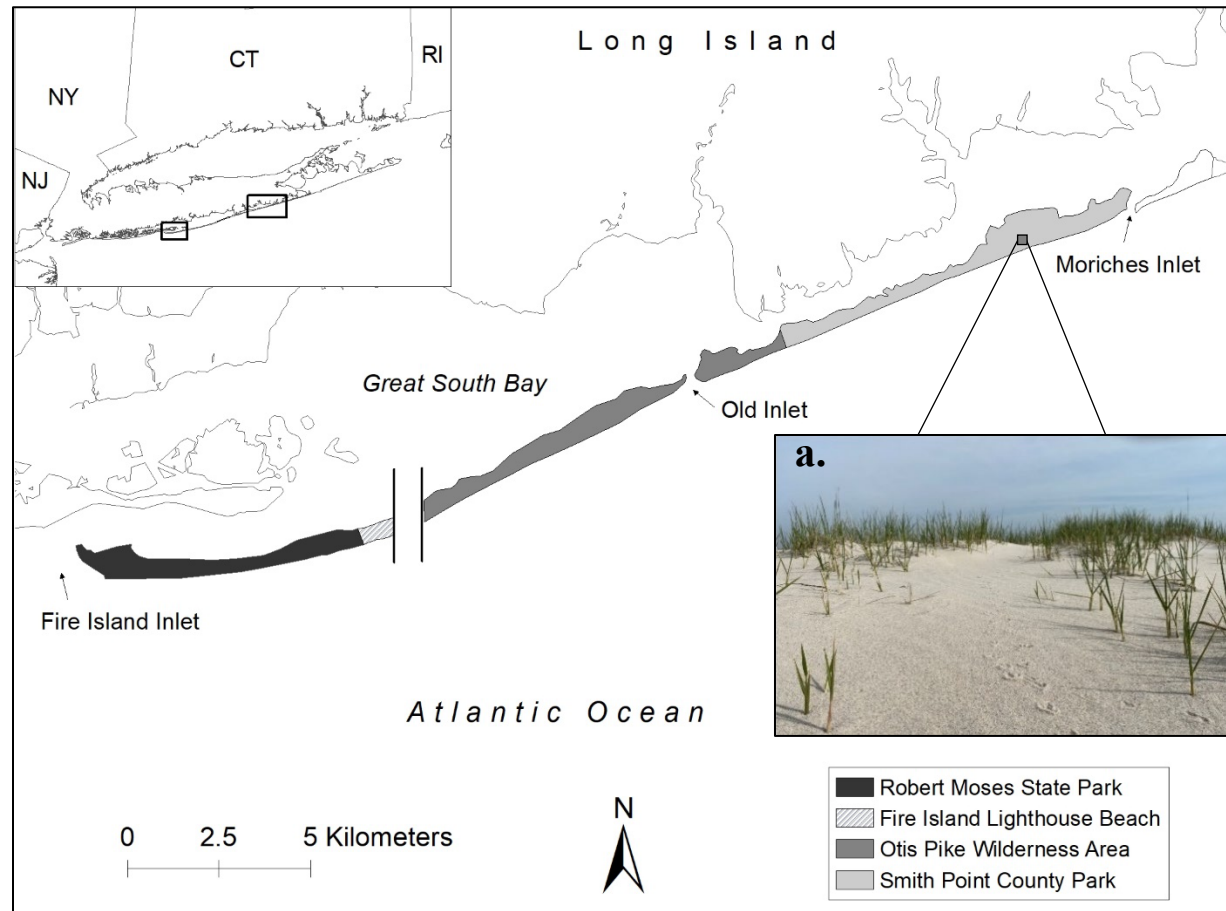
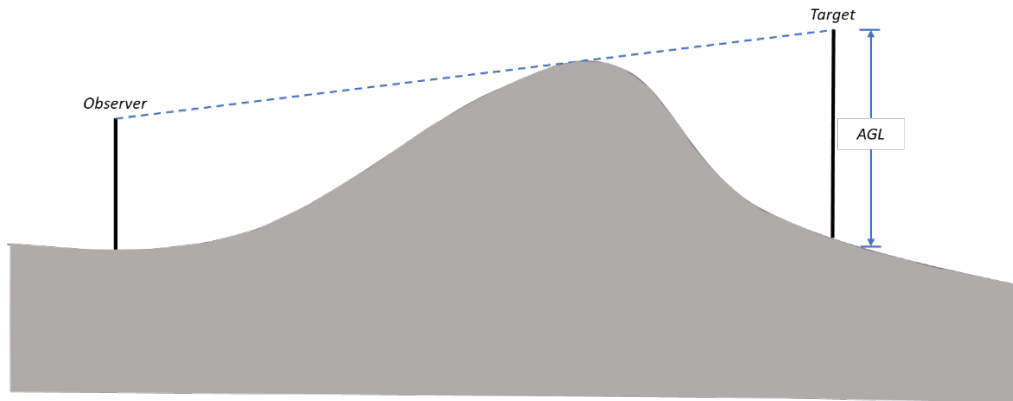
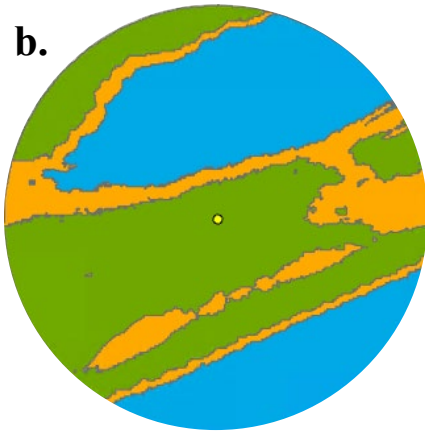


Figure 1. Map of the study area (gray) at Fire Island, NY. Fire Island is comprised of Robert Moses State Park, Fire Island Lighthouse Beach, Otis Pike Wilderness Area, and Smith Point County Park. The area between the vertical black lines comprise a 25-km long residential area excluded from the study. a) A photograph that illustrates the perspective of an adult plover facing a vegetated slope in their nesting habitat within Smith Point County Park beach on 14 April 2021.

a.



b.



c.

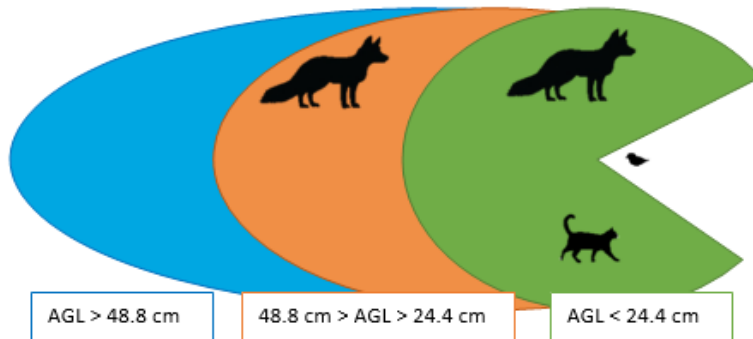


Figure 2. a) Conceptual diagram of the above ground level (AGL) setting demonstrating the height that a nonvisible target cell would need to be elevated by to become visible to the observer (figure adapted from Esri, Inc., Redlands, CA, USA). b) Example viewshed analysis output produced in ArcGIS Pro showing areas where all terrestrial predators (green), only large predators (orange), and no terrestrial predators (blue) would be visible within 30 m of an incubating plover (yellow circle). c) The above ground level (AGL) height ranges where specific predator classes would be visible to an incubating plover – $AGL \leq 24.4$ cm (green) indicates where all terrestrial predators are visible to an incubating plover; $AGL \geq 24.4$ and ≤ 48.8 cm AGL (orange) indicates where large predators are visible, but predators smaller than red fox are concealed by landscape features; $AGL \geq 48.8$ cm (blue) indicates where no terrestrial predators are visible to an incubating plover.

Appendix C. Schematic of example viewshed elevation profile

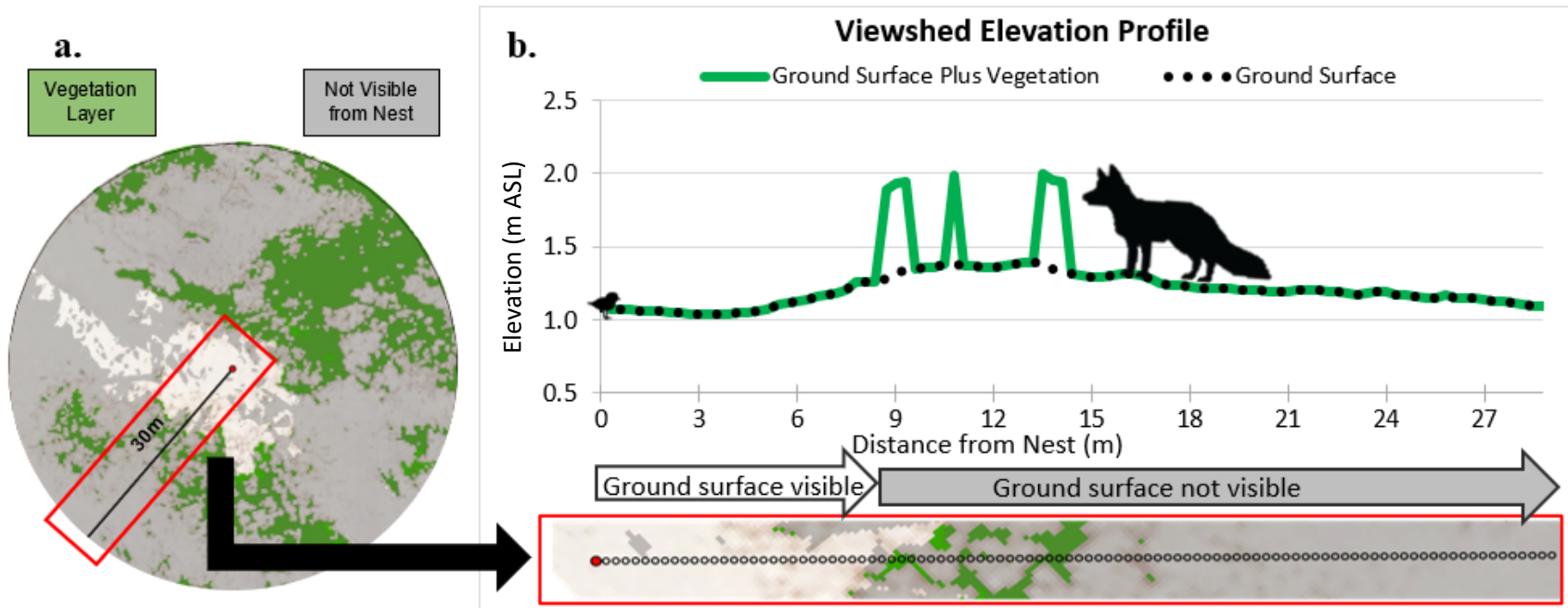


Figure C1. (a) Example ArcGIS output of viewshed analysis within a 30-m buffer of the center point showing areas not visible due to vegetation height or elevation changes in gray and vegetation coverage in green. (b) Example cross-section of obstruction.

CONCLUSION

Following the large-scale geomorphic alterations caused by Hurricane Sandy in 2012 (Halverson and Rabenhorst 2013, Sopkin et al. 2014), ongoing changes persisted in the landscape, particularly evident in the vegetation distribution on Fire Island, New York. This research revealed insights into the nesting habitat dynamics and behavior of the piping plover navigating an environment undergoing ecological succession (Bellman 2018) and experiencing a disease-driven extirpation of a primary terrestrial predator (Black 2021). I assessed changes in vegetation cover within the nesting habitat post-hurricane, evaluated how plovers responded to changes in habitat suitability over a decade, validated the significance of viewshed to see predators in plover nest site selection, and identified topographic changes as a primary source of visual obstruction to see these predators. The findings emphasize the necessity of employing updated methods for habitat assessment and monitoring to gain deeper insights into the real-life situations of these shorebirds in their habitats.

In my first chapter, I describe the changes in nesting habitat suitability and vegetation succession between pre- and post-hurricane periods. The comprehensive analysis of vegetation change indicated a 11.5% increase in vegetative cover across the landscape during the post-hurricane period of little to no disturbance. Notably, during this period median vegetative cover at nesting sites surged from 0.1% to 6.2% over five years. Our evaluation of coastal vegetative change post-hurricane coincides with similar investigations into vegetation recovery speed and distribution (Lucas and Carter 2013, Carter et al. 2018, Velasquez-Montoya et al. 2021). Measuring land cover changes over time and after significant events, including recovery phases, holds significance for effective land management strategies and for comprehending the intricate

relationship between physical, biological, and environmental processes influencing the development of coastal areas (Velasquez-Montoya et al. 2021).

Despite consistent selection patterns for several other habitat variables post-hurricane, the nesting sites in our study exhibited a distinct shift from before to after the hurricane, being positioned farther from human development and closer to bay areas after the storm compared to pre-storm. Plovers have been noted to select nests farther from human disturbance (Wilcox 1959, Robinson et al. 2021), and closer to lower energy bayside intertidal zones (Elias et al. 2000, Walker et al. 2019) than would be expected at random. Moreover, while suitable nesting habitat was greatest when we assessed immediately after stabilization, it progressively declined in subsequent years, and nests were increasingly within regions classified as unsuitable. The use of unfavorable habitats could suggest plovers exhibiting site-dependent selection, first occupying the highest quality territories and then only using lower quality territories, with demographic consequences, when high quality areas are occupied (Rodenhouse et al. 1997, Friedrich et al. 2015). The findings of this study underscore the dynamic and evolving nature of nesting habitat preferences in response to coastal landscape alterations, which are expected to become more frequent with sea level rise and increased storm events (Ezer and Atkinson 2014, Little et al. 2015, Zeigler et al. 2022). Changes in the amount of high quality habitat can lead to shifts in dispersal behavior (Rioux et al. 2011) and impact demographic factors (Catlin et al. 2019), in addition to shifting nesting behavior.

The second study delved into predator-prey dynamics influencing nesting site selection behaviors of piping plovers. Investigating the association between the visible area from the nest, or viewshed, and nest site selection, I discovered that plovers actively chose sites with enhanced predator visibility, facilitating improved predator detection. Our results validate earlier

hypotheses regarding the reason for plover's selection for open habitat (Burger 1987, Prindiville Gaines and Ryan 1988, Espie et al. 1996). If the predator remains undetectable or unseen, birds are less likely to identify the predator itself (Whittingham et al. 2004), potentially elevating the risk of nest predation.

Initially influential, the viewshed factor's effect weakened over time as ecological succession transformed the study area. We offered three reasons – supported by similar studies – for this shift ranging from individual plovers prioritizing other habitat factors that compromise nest visibility (see Cheng et al. 2023), the population growing amidst reduction in availability of sites with greater visibility (see Potts et al. 1980), and the removal of the plover's main predator, the red fox, might diminish the need for open views to detect foxes over time (referred to as predator-induced plasticity). A decrease in their historic predator numbers and the emergence of aerial predators relying on visual prey search might shift the role of cover and camouflage in plover nest site selection prioritizing predator avoidance over detection.

Topographic variation was the primary visual obstruction at plover nest sites, which was contrary to predictions that it would be the vegetation (Dwernychuk and Boag 1972, Cairns 1982, Prindiville Gaines and Ryan 1988, Espie et al. 1996, Lomas et al. 2014, Laidlaw et al. 2020). While microtopography's role in hindering predator-prey visibility has been acknowledged (Andersson et al. 2009), this study represents the initial examination of its impact specifically on ground-nesting birds as a form of visual obstruction.

Together, these studies emphasize the relationship between landscape alterations and species-specific behaviors in shaping nesting habitat preferences. Chapter 1 demonstrates a plover's ability to adapt its nesting site preferences based on changing landscape dynamics emphasizes the importance of long-term assessments in understanding species responses to

environmental shifts, while Chapter 2 highlights the balance between predator avoidance and predator detection strategies in nesting habitat selection, revealing how ground-nesting birds, like plovers, adapt their behaviors to mitigate predation risks. This study contributes to the exploration into the interplay of the physical environment with predator dynamics (Zharikov et al. 2009). Furthermore, the findings stress the significance of considering not only habitat characteristics but also predator visibility in land management strategies aimed at conserving vulnerable ground-nesting bird populations.

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