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Piping plover habitat and demography following storm-induced and engineered landscape change

Samantha Grace Robinson

Dissertation submitted to the faculty of the Virginia Polytechnic Institute and State University in partial fulfillment of the requirements for the degree of

Doctor of Philosophy

In

Fisheries and Wildlife Conservation

James D. Fraser (Co-Chair)

Daniel H. Catlin (Co-Chair)

Sarah M. Karpanty

Stephen P. Prisley

March 19, 2020

Blacksburg, Virginia

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Piping plover habitat and demography following storm-induced and engineered landscape change

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ACADEMIC ABSTRACT

Understanding the effects of large-scale disturbances and associated management actions on imperiled species can increase conservation value of future management. Piping plovers (*Charadrius melodus*; plover) are federally threatened and endangered, disturbance-dependent shorebirds, nesting on broad, sparsely vegetated beaches, sandbars, and lakeshores. In October 2012, Hurricane Sandy storm surges cleared vegetation and opened old and new inlets through Fire Island and Westhampton Island, New York, creating plover habitat. Storm effects prompted an island-wide stabilization project, and certain sections of Fire Island were designed to create and/or improve plover habitat (hereafter, restoration areas) to mitigate possible habitat loss or degradation. Many plover populations range-wide appear to be habitat-limited, and we anticipated positive population growth following habitat creation.

To help predict what might happen to the plover population following Hurricane Sandy, we evaluated the effects of habitat-creating events at several other locations in the range, evaluating the hypothesis that plover population sizes are habitat limited. We estimated the amount of habitat available before and after four significant storm and flooding events by classifying pre- and post-disturbance aerial imagery and evaluated the population changes that occurred after disturbance-related habitat alterations. Following these habitat creating events, nesting habitat increased 27%–950%, and, subsequently, these plover populations increased overall 72%–622% (increase of 8–217 pairs in 3 to 8 years after the disturbance, average 12–116% increase annually). The demographic changes likely were driven by some combination of productivity and immigration occurring simultaneously with regional increases.

We then evaluated population and suitable habitat change on Fire Island and Westhampton Island following Hurricane Sandy. We developed an integrated population model to determine the primary contributors to population dynamics and assessed the effect of restoration areas on demographic processes during 2013–2018. We also recorded individual locations of adults (2016–2018) and pre-fledge chicks (2013–2019) to evaluate effects of post-Hurricane Sandy landscape features on resource selection of adults and chicks, and behavior and survival of plover broods. We also evaluated whether breeding stage (pre-breeding, nesting, brooding, post-breeding), simple breeding stage (breeding, not-breeding), or instantaneous behavior class (parental, non-parental) best explained habitat selection during the 5-month plover breeding season.

We observed positive population growth in three of five years and overall growth through the study ($\bar{\lambda}=1.12$). Immigration and reproductive output were correlated with population growth ($r = 0.93$ and 0.74 , respectively). Compared to the rest of the study area, restoration areas had higher chick survival but lower nest survival and breeding fidelity, and population growth ($\bar{\lambda}=1.09$) in restoration areas was similar. For adult plovers, behavior class best explained habitat selection. Compared to non-parental plovers, plovers engaged in parental behavior (incubating, brooding, and accompanying chicks, hereafter ‘parental’) selected areas closer to bay intertidal habitats and with more dry sand. Non-parental plovers avoided areas with more dry sand and did not select for or against bay intertidal habitats. Additionally, non-parental plovers avoided development more than parental plovers and avoided areas of lower elevation more than parental plovers. In each year, there was more suitable habitat for parental plovers than non-parental plovers. Plover broods selected for flatter sites with less vegetation but selected for sites farther from development as time since Hurricane Sandy increased. Chick foraging rates were highest in

moist substrates and were negatively influenced by nesting plover density. Chick survival was negatively influenced by nesting plover density and was greater for earlier hatched broods. Further, chick survival was higher following an outbreak of sarcoptic mange that greatly reduced the local red fox (*Vulpes vulpes*) population.

Because immigration and local reproductive output, given fairly constant adult survival, were the primary drivers of population growth on Fire Island and Westhampton Island, efforts to increase immigration of novel breeding adults into the system, primarily by habitat creation or maintenance, are likely to have the greatest effect on local population growth. Maintaining open habitat below the 50% vegetation threshold will preserve habitat suitability and reduce local plover densities which will positively influence habitat for adult plovers throughout the breeding season, in addition to plover chick survival and foraging rates. Reduction of human interventions such as beach stabilization will allow continuous disturbance of habitats, and naturally remove vegetation. However, efforts to increase immigration may not improve regional population persistence if habitat creation is only local, therefore, management to improve reproductive output, which also has a positive effect on population growth but will also benefit regional populations through emigration, is needed. As we found that broods following the outbreak of sarcoptic mange had higher survival to fledge, maintaining the low red fox population will likely improve population growth. Regional habitat enhancement projects, such as restoration area creation, can be used to bolster plover populations and temporarily reduce local plover densities. Future restoration efforts could use the larger restoration area in this study as a model, although design criteria could be improved to increase access to moist, flat, low energy foraging sites and vegetation management will be necessary to maintain vegetation below the suitability threshold. When improving or creating plover habitat, managers should consider habitat needs of plovers of

all life stages. Habitat management should focus on maintaining vegetation-free sand and access to low-elevation foraging habitat. Allowing hurricanes such as Hurricane Sandy to alter the landscape naturally will create these landscape features.

Piping plover habitat and demography following storm-induced and engineered landscape change

Samantha Grace Robinson

GENERAL AUDIENCE ABSTRACT

Piping plovers (*Charadrius melodus*) are federally threatened and endangered shorebirds that nest on sandy beaches, sandbars, and lakeshores. In October 2012, Hurricane Sandy created substantial habitat on Fire Island and Westhampton Island, New York, which could have acted as plover habitat. However, concerns about mainland safety from future storms prompted an island-wide project, building dunes planted with beach grass, to improve the ability of Fire Island to protect the mainland. However, planted dunes had the potential to negatively affect newly created habitat, and certain sections of Fire Island were designed to create plover nesting habitat. Because of the natural and engineered habitat creation, we predicted that the population would increase.

To illustrate that habitat creating events lead to plover population increases, we used freely available aerial imagery and identified all areas of dry and moist sand in study areas. We then used local plover monitoring data to relate habitat change to plover population change and found that for several hurricanes and floods in the piping plover range, habitat increases led to population increase. We then evaluated population change on Fire Island and Westhampton Island, and found that the population increased 90% following Hurricane Sandy, and the increase was primarily due to new immigrant adults, and local reproductive success. The created restoration areas had similar reproductive output and population growth to the rest of the study area.

To determine the areas on Fire Island and Westhampton Island that were adequate habitat for piping plover adults, we compared habitat used by plovers to what was available on the

island. Because the plover breeding season is dynamic in that birds move through breeding stages that may have different constraints, and because habitat protections are typically only focused on breeding stages, we evaluated differences in habitat selection by breeding stage and behavior. We determined that habitat use differed between adults exhibiting parental behaviors and adults exhibiting all other behaviors. Non-parental plovers avoided dry sand. Both parental and non-parental plovers avoided development and high elevation sites. Overall, more sand was suitable for parental plovers than non-parental plovers. Because reproductive output also was influential to the population increase on Fire Island, we evaluated effects of landscape features on plover chick habitat, foraging, and survival. Plover chicks avoided vegetation, and selected flatter areas, but selected sites closer to development as time since Hurricane Sandy increased. Chicks spent more time foraging in moist substrates, and less time foraging when there were more plovers nesting in a management unit. Chick survival also was lower when more plovers were nesting in a management unit and was greater for earlier hatched broods. Further, chick survival was higher following sharp declines in the local red fox (*Vulpes vulpes*) population due to outbreaks of sarcoptic mange.

Overall, Hurricane Sandy was a positive force for this local plover population and local efforts to allow hurricane storm surges to modify the island in the future will improve long-term population persistence. Efforts to increase immigration of novel adults into Fire Island and Westhampton Island, primarily by habitat creation or maintenance, are likely to have the greatest local effect on positive population growth. Improving reproductive output is likely to have a positive effect on local and regional population growth, particularly by maintaining a low red fox population, if there is suitable habitat to support recruits. Further, we are beginning to see negative effects of nesting plover density on chick survival and foraging, which may suggest this

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Table H1. Model selection table determining whether slope or elevation better described variation in piping plover chick resource selection. The top variable was included in all resource selection models to evaluate piping plover brood habitat selection 2014–2019 on Fire and Westhampton Islands, NY.	227
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ATTRIBUTIONS

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

Chapter 1: Irruptions: evidence for breeding season habitat limitation in Piping Plovers

James Fraser, Daniel Catlin and Sarah Karpanty (Department of Fish and Wildlife Conservation, Virginia Tech) provided support and substantially edited the manuscript. Jon Altman (Cape Lookout National Seashore, National Park Service), Ruth Boettcher (Virginia Department of Game and Inland Fisheries), Kevin Holcomb (Chincoteague National Wildlife Refuge, U.S. Fish & Wildlife Service), Coral Huber (Omaha District, United States Army Corps of Engineers), Kelsi Hunt (Department of Fish and Wildlife Conservation, Virginia Tech), and Alexandra Wilke (The Nature Conservancy) collected the data and provided edits to the manuscript. This work was previously published in *Avian Conservation and Ecology* and is used here with permission (Appendix H).

Chapter 2: Piping Plover population change in a hurricane affected population and the relation to constructed nesting habitat

Daniel Gibson (Department of Fish and Wildlife Conservation, Virginia Tech) provided analytical support and substantially edited the manuscript. Thomas Riecke (Department of Natural Resources and Environmental Science, University of Nevada) provided analytical support and edited the manuscript. James Fraser (Department of Fish and Wildlife Conservation, Virginia Tech) secured funding and provided substantial edits to the manuscript. Henrietta Bellman, Audrey DeRose-Wilson, and Katie Walker (Virginia Tech, Department of Fish and Wildlife Conservation) helped collect data and edited the manuscript. Sarah Karpanty (Virginia Tech, Department of Fish and Wildlife Conservation) provided support and substantially edited

the manuscript. Daniel Catlin (Virginia Tech, Department of Fish and Wildlife Conservation) secured funding, provided analytical support, and provided substantial edits to the manuscript.

Chapter 3: Differential habitat suitability between behavioral classes in adult piping plovers

Katie Walker and Henrietta Bellman (Virginia Tech, Department of Fish and Wildlife Conservation) helped collect data and edited the manuscript. Daniel Catlin (Virginia Tech, Department of Fish and Wildlife Conservation) secured funding, provided analytical support, and provided substantial edits to the manuscript. Sarah Karpanty (Virginia Tech, Department of Fish and Wildlife Conservation) provided support and substantially edited the manuscript. Shannon Ritter (Virginia Tech, Department of Fish and Wildlife Conservation) conducted all landcover classifications and maintained the GIS database. James Fraser (Department of Fish and Wildlife Conservation, Virginia Tech) secured funding and provided substantial edits to the manuscript.

Chapter 4: Linking piping plover chick ecology to landscape features in a post-hurricane landscape

Katie Walker and Henrietta Bellman (Virginia Tech, Department of Fish and Wildlife Conservation) helped collect data and edited the manuscript. Daniel Gibson (Department of Fish and Wildlife Conservation, Virginia Tech) provided analytical support and substantially edited the manuscript. Daniel Catlin (Virginia Tech, Department of Fish and Wildlife Conservation) secured funding, provided analytical support, and provided substantial edits to the manuscript. Shannon Ritter (Virginia Tech, Department of Fish and Wildlife Conservation) conducted all landcover classifications and maintained the GIS database. Sarah Karpanty (Virginia Tech, Department of Fish and Wildlife Conservation) provided support and substantially edited the

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INTRODUCTION

Human-induced landscape changes can have important, long-lasting effects on ecosystem processes (Smith 2007, Haddad et al. 2015). One type of landscape change is alteration of normally dynamic landscapes, where humans have transformed or halted natural processes (Hunter et al. 2001). Fire suppression, reduced variability in river processes with channelization and dams, and reduction in natural grazing regimes all alter the natural process of previously dynamic systems (Bragg and Hulbert 1976, Hunter et al. 2001, Nilsson et al. 2005).

Few ecosystems are as dynamic as barrier islands: low-lying sandy landforms adjacent to coasts across much of the world, and make up a significant contribution to coastal ecological services (Leatherman 1988, Stutz and Pilkey 2001, Pilkey and Fraser 2003). Wave energy annually rolls sand over barrier islands, burying vegetation, building dune systems, and moving islands landward (Moore and Murray 2018). Barrier island shape also is in constant flux, particularly at inlets and on oceanfront beaches (Leatherman 1988). Barrier islands in the United States are frequently used for agriculture, human recreation, industry, and some are stable enough to maintain resorts, housing, and transportation systems like major roadways (Buerger et al. 2000, Stutz and Pilkey 2005, McNamara and Werner 2008). On the east coast of the United States, barrier islands occur in nearly every state and are highly variable in size, shape, and geomorphic dynamics.

Due to the dynamic nature of barrier island systems and the presence of infrastructure, barrier islands have long been stabilized (e.g., >100 years in Galveston Texas, >200 years on Coney Island, NY; Pilkey and Fraser 2003) to prevent or reduce island migration, storm impacts, and to allow for long-term infrastructure (Stutz and Pilkey 2005). Hard stabilization of barrier islands includes seawalls, jetties, and groins (Hall and Pilkey 1991). Beach nourishment and dune

creation coupled with planting of stabilizing plants also are techniques to stabilize barrier islands (Charbonneau et al. 2016). Ultimately, barrier island stabilization can lead to narrowing of beaches (Hall and Pilkey 1991), and with the increasing threat from climate change, barrier islands may not be able to respond to rising sea levels quickly enough to persist if hard stabilization is too extensive (Feagin et al. 2010). The inability of barrier islands to respond to a changing climate may threaten the ecosystem dynamic of these sites (Moore and Murray 2018).

Fire Island and Westhampton Island, barrier islands off the south shore of Long Island, New York, support generally seasonal human populations and federal, state, and county parks and have experienced widespread geomorphic change throughout the decades (Schwab et al. 2000). These islands also have several types of stabilization (e.g., beach nourishment, jetties, stabilizing dunes, Kratzmann and Hapke 2012, Brenner et al. 2018). Although effects of stabilization and climate change on barrier islands dynamics and persistence are important, we also should consider the effects of stabilization on non-human species using dynamic landscapes (Schmiegelow and Mönkkönen 2002).

Fire Island and Westhampton Island support breeding populations of a variety of nesting shorebirds and seabirds, such as piping plover (*Charadrius melodus*, hereafter plover), least tern (*Sternula antillarum*), willet (*Tringa semipalmata*), and American oystercatcher (*Haematopus palliatus*). The islands also support seabeach amaranth (*Amaranthus pumilus*), a federally threatened plant, migratory populations of the federally threatened rufa red knot (*Calidris canutus rufa*), and many other migratory birds (Monk et al. *in revision*, Kwon et al. 2018, Walker et al. 2019). Many of the species on Fire Island and Westhampton Island are early successional and require regular landscape disturbance to maintain open habitats (Zeigler et al. 2019). The protection on the island for the breeding birds includes string fencing on posts that

excludes public access to nesting sites. Some areas are open to driving and these sites are typically closed once shorebird chicks hatch (DeRose-Wilson et al. 2018). However, protection of foraging areas and areas that are not previously known for nesting is limited (Walker et al. 2019).

Piping plovers are relatively small (approx. 55g) shorebirds that breed from North Carolina to Canada on the Atlantic Coast (Elliot-Smith and Haig 2004). They were listed as threatened under the Endangered Species Act in 1986 (USFWS 1985) due to habitat loss, predation, and human disturbance (USFWS 1996). Plover nesting habitat generally is wide, sparsely vegetated dry sand, ideally with access to bayside intertidal habitat for foraging. They select sites with low wave energy intertidal habitats and ephemeral pools (Elias et al. 2000). Plovers are territorial on the breeding grounds (Haig and Oring 1988) and therefore local populations are limited by the number of territories that can co-occur in an area, although densities vary across the range (Hecht and Melvin 2009). Local nesting plover densities are habitat-dependent and tend to be higher in sites with access to higher quality forage (Cohen et al. 2009). Their habitats also are highly disturbance dependent, meaning that regular disturbance, generally in the form of storms and flooding, is required to maintain open, sparsely vegetated sand. When disturbance occurs, it can release plovers from existing negative density-dependent feedback, allowing reproductive output and immigration to increase, typically causing population increase (Cohen et al. 2009, Catlin et al. 2015, Hunt et al. 2018a).

Hurricane Sandy intersected the northeast Atlantic coast in October of 2012. The hurricane caused large storm surges, billions of dollars of damage to infrastructure, and loss of human life (Park et al. 2014). Hurricane Sandy storm surges made broad scale changes to the barrier islands of New York and New Jersey, specifically Fire Island and adjacent Westhampton Island (Hapke

et al. 2013). Three island breaches, where ocean water was able to flow to the bay, occurred on Fire Island and one on Westhampton Island (USFWS 2014). Additionally, storm surges carried extensive sand over portions of the island, increasing the backshore width and creating dry sand access across the island from the ocean to the bay. Three of the breaches in the island were filled in accordance with the Breach Contingency Plan (USACE 1996), but one was in the middle of a National Wilderness Area and remains open.

Following Hurricane Sandy, there was a perceived need to stabilize the island against future storms. The Fire Island to Moriches Inlet Stabilization Coastal Storm Risk Reduction Project (FIMI) was proposed, which involved widening oceanfront beaches and creating dunes planted with American beachgrass (*Ammophila breviligulata*; USACE 2014). However, due to the threatened status of the piping plover and other species on Fire Island, the United States Fish and Wildlife Services drafted a Biological Opinion to document the potential threats of the FIMI to the threatened and endangered species on Fire Island (USFWS 2014). In response to the potential detrimental effects to plovers from the FIMI, two sites were modified to act as piping plover nesting habitat (restoration areas; USFWS 2014). Vegetation management in restoration areas also was mandated under the BO. Vegetation removal would be triggered when vegetation cover in management areas reached $> 30\%$ (USFWS 2014).

The landscape changes from Hurricane Sandy, breach fills, restoration areas, and successional vegetation change could result in changes to piping plover reproductive output, specifically by affecting nest and chick survival. Landscape modifications also can result in changes in adult survival, immigration, and emigration rates (Catlin et al. 2016). These vital rates can then cumulatively cause changes in the population growth rate and breeding population size (Wilcox 1959, Cohen et al. 2009). From past habitat-creating events, we hypothesized that

reproductive output would increase due to a release from negative density dependent effects on nests and chicks (Rodenhouse et al. 1997, Hunt et al. 2018b). We expected that plovers would use the restoration areas created by the USACE, based on use of artificially created sandbars on the Missouri River (Catlin et al. 2015). We also anticipated that the population would reach carrying capacity during this study and begin to decline due to negative density-dependence (Nevoux et al. 2011, Catlin et al. 2019).

We began monitoring the affected plover population on Fire and Westhampton Islands in 2013 during the first breeding season following Hurricane Sandy. Following seven years of plover monitoring (2013–2019), we set out to understand the long-term effects of the Hurricane and subsequent alterations to the islands on the local plover population. The goal of this work was to understand the effects of engineered and storm-induced changes on Atlantic Coast piping plovers, particularly on population dynamics and by using remotely sensed, fine scale imagery.

First, we tested a proof of concept that plovers across the breeding range are habitat limited, and thus, they respond positively to habitat creation. In Chapter 1: *Irruptions: Evidence for breeding season habitat limitation*, we compiled a set of plover breeding sites where events at similar scales to Hurricane Sandy also increased the breeding population size. Where possible, we classified imagery before and after events to document habitat change and used local plover monitoring data to illustrate changes in population size and determine whether there were corresponding changes in reproductive output.

In Chapter 2: *Piping plover population change in a hurricane affected population and the relation to constructed nesting habitat*, we evaluated the population change on Fire Island, 2013–2018. We used an integrated population model to determine which demographic rate contributed the most to population change and to assess the performance of USACE restoration areas (2015–

2018) relative to the rest of the study area. In the following chapters, we took a deeper look into two specific life-stages of the breeding season on Fire and Westhampton islands based on the specific drivers of population growth rate.

In Chapter 3: *Piping plover habitat selection varies by behavior*, we used resource selection functions to determine whether adult piping plover breeding stage or behavior best described habitat selection. We then projected the resource selection functions onto annual aerial imagery to evaluate where, and by how much, habitat suitability differed by breeding stage or behavior.

Finally, in Chapter 4: *Linking piping plover chick ecology to post-hurricane landscape features*, we evaluated resource selection, behavior, and survival of piping plover chicks in the context of a variety of landscape features to determine how plover chicks responded to the changed landscape after Hurricane Sandy. We used resource selection functions to evaluate variation in habitat selection, linear mixed-effects models to test for variation in foraging rates, and young survival models to test for variation in survival.

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**CHAPTER 1: IRRUPTIONS: EVIDENCE FOR BREEDING SEASON HABITAT LIMITATION IN PIPING
PLOVER (*CHARADRIUS MELODUS*)**

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Irruptions: evidence for breeding season habitat limitation in Piping Plover (*Charadrius melodus*)

Samantha Robinson¹, James Fraser¹, Daniel Catlin¹, Sarah Karpanty¹, Jon Altman², Ruth Boettcher³, Kevin Holcomb⁴, Coral Huber⁵, Kelsi Hunt¹, and Alexandra Wilke⁶

¹ Department of Fish and Wildlife Conservation, Virginia Tech

² Cape Lookout National Seashore, National Park Service

³ Virginia Department of Game and Inland Fisheries

⁴ Chincoteague National Wildlife Refuge, U.S. Fish & Wildlife Service

⁵ Omaha District, United States Army Corps of Engineers

⁶ The Nature Conservancy

Abstract

Effective management of wildlife populations requires identification of the factors limiting their growth. The Piping Plover (*Charadrius melodus*) is an imperiled, disturbance-dependent shorebird species, nesting on broad, sparsely vegetated beaches, sandbars, and lakeshores. In areas minimally affected by human uses, plover habitat loss occurs through vegetation encroachment and erosion. Alternatively, habitat may be increased by sand deposition caused by storm or flood induced sediment transport or scouring that removes vegetation, or by receding lake levels. To test the hypothesis that plover populations are limited by available breeding habitat, we first estimated the amount of habitat available before and after four significant storm and flooding events (i.e., disturbance) by classifying pre- and post-disturbance aerial imagery. We then evaluated the population changes that occurred after disturbance-related habitat alterations. Additionally, we report on population changes from four population increases that occurred after habitat creation events, for which we did not have imagery suitable for

classification. The storm and flood effects considered were those from hurricanes and nor'easters on barrier islands of Virginia, North Carolina, New York, and Maryland, USA, and those from floods and high water output from the Gavins Point Dam on the Missouri River between South Dakota and Nebraska, USA. The amount of nesting habitat increased 27%–950% at these sites, and plover populations increased overall 72%–622% after these events (increase of 8–217 pairs in 3 to 8 years after the disturbance, average 12–116% increase annually). The demographic changes were driven by productivity in some cases and probably by increases in immigration in others, and occurred simultaneously with regional increases. Our results support the hypothesis that our focal plover populations were at or near carrying capacity and are habitat limited. Currently, human interventions such as beach stabilization, the construction of artificial dunes, and dams reduce natural disturbance, and therefore the carrying capacity, in many plover breeding areas. If these interventions were reduced or modified in such a way as to create and improve habitat, plover populations would likely reach higher average numbers and the potential for achieving recovery goals would be increased.

Key words: *Charadrius melodus*, density-dependence, eCognition, habitat limitation

Introduction

Habitat loss is a pervasive cause of population declines (e.g., Dolman and Sutherland 1995, Flockhart et al. 2015). When habitat is lost, or its suitability declines, density-dependent demographic responses can result in population declines (Turchin 1990, Newton 1998, Brook and Brashaw 2006, Martin 2014). When an increasing population nears the level habitat can support, often referred to as the carrying capacity of the habitat, some or all vital rates change. Birth rates and immigration may decline, and death rates and emigration rates may increase (Nicholson 1933, Newton 1998), causing population numbers to settle near the carrying capacity.

These demographic rates may be mediated by individual-specific changes related to habitat , as when transformation of body condition affects survival, or clutch size which then affects the number of local recruits available to breed in the following year (Cooch et al. 1989, Francis et al. 1992, Marra et al. 2015). If densities in available habitat limit a population, improvement of existing habitat or creation of new habitat should increase carrying capacity, thus resulting in population growth. Alternatively, some species declines have been driven by density independent factors, including climate (Putman et al. 1996), pesticides (Grier 1982, Buehler 2000, White et al. 2002, Shields 2014), poisons (Nadjafzadeh, et al. 2013) and overharvest (Chan et al. 2014, Wittemyer et al. 2014, Hamilton et al. 2015, Licht et al. 2015). In such cases, when habitat availability remained abundant or was restored, and reproduction and mortality returned to more normal levels, populations rebounded.

Failure to discern what limits a population can lead to ineffective conservation interventions. For example, if a population is limited by habitat or predators, but the primary management strategy is to increase productivity by reducing human disturbance, management may be ineffective without concurrent habitat creation or predator reduction (Baudains and Lloyd 2007). On a barrier island in North Carolina, mammalian predators were hypothesized to be contributors to American Oystercatcher (*Haematopus palliatus*) population change through nest and chick predation, but after a predator removal experiment, no relationship was detected between predator numbers and nest survival (Schulte and Simons 2016, Stocking et al. 2017). Instead, increases in nest success may have been driven by increases in habitat quality following Hurricane Isabel (Schulte and Simons 2016). Specific drivers of vital rates and abundance vary by species and location, therefore it is important to assess them on a species- and location-specific basis and at appropriate scales. If broad-scale or range-wide drivers can be identified, it

could help target effective management tasks that could lead to regional increases or even recovery.

The Piping Plover (*Charadrius melodus*; hereafter plover) is a temperate breeding shorebird that was federally listed in the U.S. as threatened and endangered in 1986 (USFWS 1985). The species has experienced broad-scale habitat loss throughout its range. Plovers are territorial, and defend nesting sites (Elliot-Smith and Haig 2004). In general, plover habitat comprises sparsely vegetated or open dry sand or gravel for nesting and moist sand for foraging (Burger 1987, Elliot-Smith and Haig 2004, Fraser et al. 2005). If breeding habitats are not periodically disturbed by storms or floods or human interventions, vegetation can quickly overcome sandy habitats and render them unavailable for plovers (Gieder et al. 2014, Zeigler et al. 2017a). Habitat loss on the Atlantic Coast has been attributed to increased development. There, infrastructure has replaced natural habitats. Moreover, to protect this infrastructure, shorelines have been manipulated in ways that inhibit natural beach renewal processes (Wilcox 1959, USFWS 1996). In the Great Plains, river management, through dams, reservoirs, and channelization has reduced available habitat for plovers on prairie rivers (Catlin et al. 2015).

Since being federally listed, range-wide productivity monitoring has been a major component of assessing the success of recovery actions, especially in human-populated areas (Hecht and Melvin 2009a). Plover monitoring generally consists of frequent surveys to locate territorial adults and nests and to determine success of hatched chicks (Hecht and Melvin 2009a). Despite intensive monitoring, management, and research, plover populations have not met the recovery goals set by the U.S. Fish and Wildlife Service (USFWS), potentially because plovers are limited by the amount and quality of available habitat on the landscape (Hecht and Melvin

2009b). However, these high quality, long-term monitoring data may be useful to assess the mechanisms of population limitation for plovers across the breeding range.

The mechanisms of density-dependent limitation in plovers may be varied, as they can involve density-dependent changes in more than one vital rate (birth, death, immigration and emigration). When below carrying capacity, reproductive output plus immigration should be higher than emigration plus mortality, but as a population nears carrying capacity these vital rates may change, slowing the population increase, or causing a decline (Hixon et al. 2002). For example, increases in density can increase the likelihood of detection of nests and chicks by predators, thereby reducing reproductive output (Catlin et al. 2011a). Plover territoriality also directly limits the maximum number of breeding pairs the habitat can support (Cairns 1982). An increase in density can reduce the immigration rate, or increase the emigration rate, by limiting the number of available territories, thereby reducing the population's growth rate (Catlin et al. 2016).

Crowding effects can reduce reproductive output as incoming birds may need to settle in lower quality habitats, thereby reducing the per capita reproductive output of the population (Pulliam 1988). Alternatively, the main effect of habitat quality on plovers may be on density, reducing reproductive output by competition for food, increasing predation, and increasing antagonistic interactions (Catlin et al. 2011b, Cohen et al. 2009). Habitat of higher quality tends to be closer to moist foraging substrate, specifically lower wave energy habitats with abundant invertebrate prey (Elias et al. 2000, Cohen et al. 2009, Walker et al. 2019), but birds can settle in areas of lower quality habitat and therefore should exhibit lower productivity or survival on average.

Discerning the causes of population change, and especially the role of density-dependence, can be challenging with the monitoring data that are obtained for most plover populations (Hecht and Melvin 2009a). For breeding plovers and other beach nesting birds, the relationship between reproduction and habitat can be confounded by human disturbance or predation (Maslo et al. 2019). For example, On Fire Island, New York, 42% of geomorphically suitable habitat was unsuitable because of intensive beach driving (Walker et al. 2019). In some areas, habitat creation and improvement has been used for plover recovery (Catlin et al. 2015), and in others, predation has been identified as a primary limiting factor, and thus lethal predator management has occurred (Patterson et al. 1990, Cohen et al. 2009, Hecht and Melvin 2009a, Catlin et al. 2011b). However, in many areas, the primary cause of population suppression and decline is unclear and difficult to identify. If, instead of predators or other factors, the amount and quality of available habitat is the primary factor limiting plover numbers (Norris et al. 2004), this could be indicated by observing population numbers before and after habitat creation. Local population changes due to density may not directly affect the regional population, however, especially if immigration is the primary driver of increase. To determine whether local immigration is a function of birds' movement to new habitat (Kokko and Sutherland 2001) or a result of a regional increase, local population change can be compared to regional population trends. If population increase on a small-scale also corresponds to population increases on a broader scale that would be systematic evidence of a population-level effect of a release of density.

Stochastic events, such as hurricanes, nor'easters, and floods can create and improve plover habitat and initially reduce nesting densities by washing away vegetation and shifting and exposing sand for nesting habitat (Walker et al. 2019, Cohen et al. 2009, Hunt et al. 2018).

Additionally, these events can create or expose highly productive foraging habitats (Le Fer et al. 2008, Cohen et al. 2009), thereby increasing the quality of the habitat and presumably the carrying capacity. In both cases, if plovers are at the carrying capacity of their habitats, and are limited mainly by availability and quality of habitat for breeding territories, a stochastic, density-independent event that creates or exposes new habitat or improves the quality of existing habitat, should be followed by increases in plover populations through immigration, reproductive output, and/or survival. In this study, we hypothesized that if breeding habitat is limiting plover populations, when habitat increases so does the carrying capacity, thus, the population should increase. To test our hypothesis, we reviewed existing information on the response of plover populations to habitat creating events and used plover data from across the species' breeding range to investigate the relationship between habitat creation from storm and flood events, plover pair counts and productivity.

Study Areas

To assess the relationship between habitat and plover populations, we selected study areas for which we knew that long-term plover monitoring data existed, and areas we knew had been affected by events, such as floods or storms, that tend to create habitat in disturbance-dependent systems. Some of the events have been previously published, such as the impact of Hurricane Isabel on Atlantic Coast plovers (Boettcher et al. 2007, Schulte and Simons 2016), and flooding on the Missouri River (Hunt et al. 2018a). All study areas had some degree of predator reduction within our focal periods, either for plover management or for sport hunting and also had intensive management of public use or limited human access.

Cape Lookout National Seashore, North Carolina

Cape Lookout National Seashore is a 90-km chain of barrier islands off the coast of North Carolina (Hillman et al. 2012). Plovers in North Carolina nest in coarse, shelly substrates and sandy overwash habitats (Cooper 1990, Kwon et al. 2018). Hurricane Isabel made landfall on Cape Lookout on September 18th, 2003, resulting in substantial changes to the environment (Sheng et al. 2010). Plovers on Cape Lookout are distributed patchily along the island, and we selected a 5.5km section that was centered on Ophelia Inlet, which was created by Hurricane Ophelia in September of 2005 (Fig. 1).

Cedar, Wreck, and Metompkin Islands, Virginia

Cedar (9.5-km long), Metompkin (10-km), and Wreck (6-km) islands are barrier islands off the coast of the lower Delmarva Peninsula in Virginia, and we classified and examined plover pair counts for the entirety of each island (Fig. 1). Plovers in Virginia nest on broad beaches with sand-shell flats (Boettcher et al. 2007). Hurricane Isabel substantially affected much of Virginia, despite not directly striking the islands (Boettcher et al. 2007). The dry sand areas of Cedar, Wreck, and Metompkin often are connected to marsh, creating moist sand between dry sand and marsh habitats, which can be attractive to foraging plovers. For pre- and post-Isabel comparison, we combined Cedar and Metompkin islands because they are adjacent (Fig. 1).

Missouri River, Gavins Point Reach, South Dakota and Nebraska

The Gavins Point Reach of the Missouri River extends 95-km south from the Gavins Point Dam (Fig. 1), and we classified imagery and examined plover pair counts for the entirety of each island. The Gavins Point Reach is the last free-flowing section of the Missouri River, below which the river is channelized. Plovers on the Gavins Point Reach nest on open and sparsely vegetated sandbars (Catlin et al. 2015, Hunt et al. 2018). We used data from two habitat-creating events on the Missouri River. The first was flooding and high water events between 1996 and

1997 (<http://www.nwd-mr.usace.army.mil/rcc/projdata/gapt.pdf>). The second was flooding and high water events that encompassed portions of the 2010 and 2011 breeding season (USACE 2012, Hunt et al. 2017, 2018). Flooding and high water levels were related to above average snowpack and rainfall (USACE 2012). These two events were the highest outflow from the dam since its completion in 1957 (USACE unpub. data).

Westhampton Island, New York

Westhampton Island is a barrier island off the south shore of Long Island, New York, currently bounded on the western end by Moriches Inlet (Fig. 1). On Westhampton Island, plovers nest on sparsely vegetated ocean and bayward sandy beaches (Cohen et al. 2006). Several storms have affected the plover nesting habitat on Westhampton Island, but most notable are the Hurricane of 1938 (Wilcox 1959), and a large nor'easter in December of 1992 (Cohen et al. 2009). The hurricane of 1938 near Moriches Inlet increased nesting sand habitat by overwashing dunes and also created a new inlet, which increased bayside foraging access for chicks along 3.5 km of the island (Wilcox 1959). The nor'easter in 1992 created a large sand spit on the bayward side of the island and removed buildings, which increased bay access and nesting habitat along 8.4 km of the island for several years following the storm (Cohen et al. 2009).

Assateague Island, Maryland

Assateague Island is a 59km-long barrier island off the eastern coast of Maryland and Virginia (Gieder et al. 2014). It encompasses Assateague Island National Seashore and the majority of the nesting habitat for plovers in Maryland, thus we used the Maryland census pair counts to examine population change (Fig. 1; A. Hecht pers. comm). Nesting habitat for plovers in Maryland includes primarily sparsely vegetated oceanfront beaches, with occasional bay access due to overwash processes (Loefering and Fraser 1995, Patterson et al. 1991, Schupp et al.

2013). Several storms in the early 1990's overwashed vegetation and created plover nesting habitat on Assateague Island, until stabilization efforts reduced probability of overwash on the island in the later 1990s, leading to vegetation encroachment and a decline in suitable habitat (Schupp et al. 2013).

Methods

Imagery Acquisition

We obtained imagery from as close in time as possible before each event. Immediately following habitat-creating events, there is typically extensive wet sand remaining from flooding and overwash. Much of the wet sand later dries to become open dry sand nesting habitat, but for image classification purposes, it would be excluded as nesting habitat if imagery immediately following the event were used. Therefore, for after each event, we selected imagery from >1 year post-event to allow short-term effects of the storm, such as extensive moist sand and soft sand covering low-lying vegetation, to settle.

For Cape Lookout National Seashore, we obtained imagery from Google Earth Pro (Google LLC, Mountain View, CA, USA). To georeference the imagery, we placed markers on four corners of the image and recorded the latitude and longitude. We then imported the imagery into ArcGIS 10.4 (ESRI 2015, Redlands, CA, USA) and georeferenced it using the four corner locations. Our pre-storm image was from February of 2003, several months before Hurricane Isabel. Our post-Isabel image was from July of 2006, the third plover breeding season following the storm.

For the Virginia barrier island sites, we acquired imagery pre-Isabel from the Virginia Base Mapping Program, 0.61-m resolution (February–April 2002; VBMP 2002). Post-Isabel imagery was from the National Agriculture Imagery Program (NAIP), 2-m resolution (U.S.

Department of Agriculture 2016). The post-Isabel imagery for Cedar and Metompkin islands is from June 2005, and for Wreck Island is from May 2006 (U.S. Department of Agriculture 2016).

For the Missouri River, we used pan-sharpened multispectral QuickBird 1-m resolution imagery from 2009 and 2014 (DigitalGlobe Inc., Sunnyvale, CA, USA). Imagery was collected between July and September in both years.

For the remainder of our sites, comparable high resolution images corresponding with the timing of events was not available for classification. Therefore we discuss the population changes following events similar to those described here for which we do have habitat, but without estimation of area of nesting habitat or plover density.

Image Classification

For all of the irruptive events we studied and for which we had high resolution imagery, it was clear from visual interpretation of the imagery that there was more dry sand following the events that overwashed the islands and sandbars. However, to estimate the density of plovers, we needed to estimate the amount of nesting habitat available for plovers. To classify imagery, we used eCognition Essentials (Trimble, Westminster, CO, USA), an object-based classification software. We classified each image into 5–10 classes, depending on apparent spectral values within the imagery and collapsed the classification into four classes: dry sand, moist sand, vegetation, and water. We clipped each image to the ocean mean high water line, to reduce classification error due to the similar spectral signature of bright dry sand and waves.

Classifications of imagery collected outside of the growing season, such as in February or March, are likely to underestimate the amount of vegetation during much of the breeding season, but they may better represent the conditions that birds find when they arrive on the breeding grounds than would imagery collected during the growing months (i.e., June or July). Because fine-scale imagery is not readily available for all years or seasons, the timing of imagery needs to

be considered when comparing among months and years. For both Cape Lookout and the Virginia barrier islands, the pre-hurricane imagery was collected during the winter and early spring (February–April) before the growing period. The post-event imagery for all sites was collected during the growing season (May–August). Therefore, there was likely more dry sand created than we are estimating.

The Missouri River imagery was classified using Definiens Developer Software (Trimble Inc., Westminster, CO, USA). We grouped the landcover classes of the classified imagery into nesting habitat (dry sand, dry sand sparse vegetation, moist sand, moist sand sparse vegetation; Strong 2012), vegetation, water, and other (e.g., clouds, unclassified, development).

We randomly selected 200 polygon objects from each image to estimate classification error, following methods by Radoux et al. (2011). Although it was important that our images were classified accurately, our main interest was that the dry sand classification was accurate, as those areas were considered available for plover nesting.

Piping Plover Data

We obtained nesting information for all of the study areas from the agencies that monitor populations of Piping Plovers at those sites (*viz.*, The Nature Conservancy, Virginia Department of Game and Inland Fisheries, United States Fish and Wildlife Service, United States Army Corps of Engineers, and National Park Service). Plover nests typically were found by visually searching an area or by observing nesting activities such as defensive or parental behaviors. Nests were monitored at varying intervals until hatch or failure. We collected nest locations using hand-held GPS units. It is possible that nests and pairs were missed, however, we assumed that any bias would be systematic within sites. If a nest hatched, we monitored chicks until they could no longer be found or until chicks fledged. We used pair or adult counts from 2–3 years before, and 3–5 years after each habitat-creating event to examine plover abundance at all sites.

We also calculated the average percent increase for each site during the years the population was increasing. We also acquired information regarding regional population change and reproductive output for each site, to better inform the effect of our focal events on overall plover population change and progress toward recovery goals.

The total number of chicks fledged divided by the number of pairs n is the chicks/pair estimate and was used as an index for annual productivity. We used chicks/pair to evaluate reproductive output for each site and evaluated chicks/pair in reference to the estimated productivity needed for a stationary population, which is used as an average recovery threshold for Atlantic Coast plovers (1.2 chicks/pair; Melvin and Gibbs 1996). Finally, where applicable, we calculated nesting density as the number of pairs/hectare, using the nesting habitat estimate from our habitat classifications and the pair counts in the year of our classified imagery. For irruption events occurring prior to the 2000's, we lacked both high resolution plover data and high enough resolution imagery to classify for plover nesting. Therefore, we present these population increases that occurred after habitat-creating events as additional evidence for habitat limitation but cannot estimate habitat change.

Results

Across all sites, the percentage of training samples correctly classified was 87.6–98.7% for dry sand polygons. Overall accuracy was between 68.9% and 95.3%, with most misclassification occurring between moist sand and vegetation.

Cape Lookout, North Carolina

Nesting habitat in our study site at Cape Lookout increased 27% between 2003 (78.6 ha) and 2006 (100.1 ha). Following Hurricane Isabel, dry sand nesting habitat extended from the ocean intertidal to the bayside intertidal, whereas previously, access for a walking plover chick to the

bayside intertidal was mostly impeded by vegetation (Fig. 2). In the breeding season prior to Isabel, the summer of 2003, Ophelia Inlet study area had only five pairs. There were 20 pairs in the Ophelia Inlet area in 2006, a 300% increase and 26 in 2008 (420% increase; Fig 3). During the period of population increase, the average annual increase was 41% (SE = 11.2). Pair density increased from 0.051 pairs/ha in dry sand nesting habitat in 2003 to 0.24 pairs/ha in 2006.

Reproductive output in the Ophelia Inlet study area prior to and following Hurricane Isabel never exceeded the estimated value required to maintain a stationary population for Atlantic coast plovers (1.2 chicks/pair; Fig. 4). Reproductive output following the storm was at or near what is required for a stationary population (1.10–1.23), but dropped well below the estimated value needed for stationarity after 2006. Following Hurricane Isabel, the entire population of North Carolina increased 167%, from 24 pairs in 2003 to 64 pairs in 2008 (USFWS 2017). Regionally, from North Carolina to Delaware, reproductive output was higher than what is required to maintain a stationary population prior to and following Hurricane Isabel (1.22–1.95).

Cedar and Metompkin Islands, Virginia

On Cedar and Metompkin islands, dry sand habitat increased from 229.7 ha in 2002 before Hurricane Isabel to 293.1 ha in 2005, two years after Hurricane Isabel (27.6% increase, Table 1, Fig A1.1, Fig A1.2). Corresponding with the habitat increase, pairs on Cedar and Metompkin increased from 57 pairs in 2003 to 98 pairs in 2008 (72% increase, Fig. 3). While the population was increasing after Hurricane Isabel, the average annual increase was 11.8% (SE = 4.6). Pair density increased from 0.23 pairs/ha in 2002 to 0.29 pairs/ha in 2005. Reproductive output on Cedar and Metompkin Islands was above that required for a stationary population the breeding season prior to Hurricane Isabel and remained above this level for three years following the Hurricane (1.39–2.03 chicks/pair; Fig. 4). Similar to Cedar and Metompkin Islands, the entire

Virginia population increased 68%, from 114 pairs in 2003 to 192 in 2005 following Hurricane Isabel (Boettcher et al. 2007).

Wreck Island, Virginia

Dry sand habitat on Wreck Island increased from 32 ha in 2002 to 73.1 ha in 2006 (128% increase; Table 1, Fig A1.3). Prior to Hurricane Isabel, there had not been plovers nesting on the island since 1997, but plovers recolonized the island in 2004, and reached a maximum of eight pairs in 2007. From 2004–2007, the average population increase per year was 95.8% (SE = 37.5). Density increased from 0 pairs/ha to 0.08 pairs/ha in 2006. Due to the low number of pairs and logistical challenges, reproductive output was not monitored on Wreck Island during the post-Isabel years. The Wreck Island birds were part of the Virginia population increase described for Cedar and Metompkin Islands above.

Missouri River, South Dakota and Nebraska

High water in 2010 and a 2011 flood on the Missouri River affected both available habitat and nesting plovers. The flood in 2011 encompassed the entire breeding season, and left no habitat for nesting birds. There was 119.2 ha of dry sand nesting habitat in 2009 before the events and 1250.9 ha after in 2014 (950% increase). The year before the high water events in 2010, there were 119 nesting pairs in this stretch of the river. Following the flood, the number of nesting pairs decreased initially, to 68 pairs in 2012 (-57%) and peaked at 285 pairs in 2016 (319% increase over 2012; Fig. 3). The average annual percent increase from 2013 to 2016 was 43.6% (SE = 7.2%). Pair density decreased from 1 pair/ha to 0.095 pair/ha in 2009 and 2014, respectively (Table 1). Following the events, reproductive output on the Gavins Point Reach was above the reproductive output required for a stationary population needed in every year (Fig. 5). Pair counts on Missouri River from the Fort Peck Dam in Montana to the Gavins Point reach

(approximately 1300 km) also increased from 453 pairs in 2009 to 916 pairs in 2016 (102% increase, USACE unpubl. data). Following the 2011 flood, reproductive output for this region of the Missouri River was 1.17–1.49 chicks/pair.

High water events on the Missouri River, documented by higher than average monthly outflow from the Gavins Point Dam in 1996 and 1997, also resulted in a population increase (GAPT Reservoir; <http://www.nwd-mr.usace.army.mil/rcc/projdata/gapt.pdf>). The population in the Gavins Point Reach in 1995 was at a low of 26 pairs before the high water events, and reached a high of 143 pairs in 2003 (450% increase), annually increasing on average 65.5% (SE = 31.0). These increases were part of a regional increase from 197 pairs in 1995 to 397 pairs in 2000. Reproductive output for the Missouri River during this time was 1–1.58 chicks/pair.

Westhampton Island, New York

We used data from two documented irruptions on Westhampton Island, New York, prior to availability of fine scale imagery. The first occurred after the hurricane of 1938. In 1937, the plover population within the study area was 9 pairs. By 1941, the population had increased 622% to 65 pairs with an average annual increase of 73.9% (SE = 33.4, Wilcox 1959).

In the same area, in 1992, a nor'easter created new nesting and foraging habitat on West Hampton Island, leading to an increase from 0 pairs before the storm to a peak of 39 in 2000. Pair density before the storm was 0 pairs/hectare. At the peak population, the density was 0.90 pairs/ha but increased to 1.05 pairs/ha the following year after a decrease in habitat (Table 1; Cohen et al. 2009). The average increase during the years the population was increasing was 37.1% (SE = 23.6). Reproductive output during this time was variable, with 4 years below what is required for a stationary population, and 4 years above what is required for a stationary population (Fig. 5). During the same time as the increase that occurred in the 1990s, the entire

New York population increased from 191 pairs in 1992 to 289 pairs in 2000 (USFWS 2016). Regional reproductive output for the New York, New Jersey area was close to, or above the reproductive output required for a stationary population (0.97–1.35) during this study period.

Assateague Island, Maryland

Nor'easters on Assateague Island in Maryland in the early 1990's also were followed by an irruption of plovers in the area, with Maryland pair counts increasing from 14 to 60 pairs between 1990 and 1997 (329% increase, Schupp et al. 2013, USFWS 2017), and annually increased on average 48.2% (SE = 10.1) during the years the population was increasing. Reproductive output on Assateague was below the estimated amount required for stationarity prior to the nor'easters. Reproductive output increased above the amount required for stationarity following the nor'easters and remained high for 4 years, although the trend was declining after 2 years (Fig. 4). Following 1997, the beach was modified to reduce further overwash, and the habitat converted to herbaceous vegetation (Schupp et al. 2013). Assateague comprises the majority of nesting habitat in Maryland, thus the increases on Assateague contributed 100% of the increase in Maryland, however the neighboring states of Delaware and Virginia either remained stationary or declined during this time period (USFWS 2016). Regional reproductive output was variable during this time period, with some years above and some years below what is required for a stationary population (0.62–1.37).

Discussion

Our findings support the hypothesis that our focal plover populations were at the carrying capacity of their habitats, such that when the amount of habitat increased, plover populations increased. Across all sites, when habitat increased the populations we monitored increased by 72%–622%, increasing on average 12–116% annually. The mechanism behind population

growth may have differed among events, as local reproductive output was not always at or above the estimated rate required for stationarity, which suggested that immigrating adults and regionally high reproductive output contributed significantly to the population increase several of the populations we studied. In every case except Wilcox (1959), where information is lacking, the population irruptions were part of regional increases, not just instances of small movements of birds that already existed in these populations.

Some storms overwash barrier island habitats and create bayside foraging habitat, and also can increase dry sand habitat (Fig. 2; Leatherman 1979, Maslo et al. 2019, Walker et al. 2019). On the Missouri River, high outflow from the Gavins Point Dam and flooding created new, un-vegetated sandbars (USACE 2012), resulting in a population increase (Fig. 3). Similarly, overwash and storm surges on barrier islands between New York and North Carolina throughout the last century created broad areas of open nesting habitat, which were followed by population increases (Fig. 3; Wilcox 1959, Cohen et al. 2009, Schupp et al. 2013). Evidence also suggests that when habitat is not created, populations remain stable or decline. This decline was observed with pair declines on Jones Island, NY, where the population declined following decrease of both nesting and foraging habitat (McIntyre et al. 2010). Similarly, plover populations on Fire Island, New York were declining until Hurricane Sandy created habitat in the fall of 2012 (Walker et al. 2019).

The density (pairs/ha) of birds from all of our Atlantic Coast study areas increased following Hurricane Isabel. Cohen et al. (2009) estimated the carrying capacity of Westhampton Island to be a density of 0.44–1.05 pairs/ha, with greater densities detected in areas where flightless plover chicks could access both ocean and bay-side foraging habitats. Our estimated densities were lower than the later Westhampton Island study in all other cases; however, most

populations were still growing in the years for which we have habitat estimates. We would need additional estimates of habitat when the populations reached carrying capacity to be directly comparable with past studies. Carrying capacity of plovers may be lower in lower latitudes (USFWS 1996, Hecht and Melvin 2009b), which would be consistent with our lower densities in Virginia and North Carolina than in more northerly populations. However, density likely initially decreased in all cases the year following the storm due to more habitat and fewer pairs than when we classified imagery.

The Missouri River plover population in 2010–2016 is our only case where post-event density was lower than pre-event densities at the time of classification following the events. The amount of habitat created by the floods was much greater than that of the Atlantic Coast cases, and even the extremely high productivity could not have produced enough birds to occupy all of the available habitat during our study. On the Missouri River, population increases were driven by increased productivity from reduced density-dependent predation on nests and chicks and competition (Hunt et al. 2018) and to a lesser extent, by immigration (Catlin et al. 2015, 2016). There was an initial detrimental effect from both the high water events in the 1990s and the high water and flooding in the 2000s. Reduced survival and low reproductive output during the flood could have also contributed to the low post-event densities. The flood in 2011 both reduced adult survival (Weithman et al. 2017, Hunt et al. 2018) and produced few recruits to colonize the newly created habitat (Hunt et al. 2018), leading to an initial population decline and a lag in the population increase. Despite the initial lag, the plover population responded with record high reproductive output and exhibited nearly exponential growth for several years before stabilizing (Hunt et al. 2018, Hunt et al. 2019).

The mechanisms behind the density-dependent population growth at the Atlantic Coast sites are less clear. In all cases except Maryland, the population immediately increased. To balance the natural mortality of these populations, an estimated annual productivity of about 1.2 chicks/pair is required (Melvin and Gibbs 1996). The immediate population increases following storm events could have been due to a reduction in density-dependent competition. An increase in nesting habitat could have allowed space for first-time breeders to find territories following regional productivity above what would be required for a stationary population the year prior to the storm, or birds that had not bred before due to a lack of available territories (Newton 1998, Fig. 4). The increase in habitat could also have allowed chicks increased access to quality foraging habitats, increasing chick survival and recruitment. However, the required number of chicks for stationarity were not produced in all years at all sites following our focal hurricanes or nor'easters, despite consistently increasing populations. Thus, immigration likely played a larger role in the Atlantic coast irruptions than the Great Plains irruptions, especially for the southern U.S. sites, where regional reproductive output was high (1.63 chicks/pair) the breeding season prior to Hurricane Isabel (Fig. 4; USFWS 2016). The difference in apparent contribution from immigration between the Great Plains and the Atlantic Coast also may be a function of the spatial scale of our investigation, as an area's apparent immigration rate is affected by its size. In large study areas, individuals settling may be regarded as natal recruits, whereas in a tiny area, most will be classed as immigrants (Newton 1998). The Gavins Point Reach of the Missouri River is ten times the size of any of the other study sites. Therefore, small local movements, such as an adult moving to different nesting sandbars between years, would not be considered immigration or emigration.

A study in Eastern Canada, near the northern end of the Atlantic Coast range, found that following winter storms similar to Hurricane Isabel and the nor'easters reported here, the number of fledglings increased (Bourque et al. 2015). However, Bourque et al. (2015) did not find a strong relationship with pair counts, suggesting that the amount of habitat created following their storms was too little to significantly change the amount of available nesting habitat given the present population, but did allow for more foraging habitat for pre-fledged chicks. Alternatively, other factors could be affecting this population's growth rate, such as factors outside of the breeding season.

The effects of several of the events observed in this study also were seen at broader scales. Westhampton Island only contributed 40% of the regional increase in New York, and regional reproductive output likely also contributed birds to the local increase in some years. The overall pair increase we documented on Cedar, Wreck, and Metompkin islands accounted for 79% of the Virginia's population increase, and only 55% of the pair increase in North Carolina came from our focal area on Ophelia Inlet. Regional reproductive output was high, and thus also likely supplied birds to settle into the newly created habitats at both the Virginia and North Carolina sites following Hurricane Isabel, further suggesting that birds were not just moving around within the region. The irruption on the Missouri River in the 1990s only contributed 23% to the regional increase, and similarly in the 2000s, only 36% was from the Gavins Point Reach (USACE unpubl. data), and in general, regional reproductive output was high following both events. That the irruptions were evident at both fine and broad scales, provides evidence that the increases were widespread, likely from habitat also being created at nearby sites other than the ones we focused on here, rather than adults shifting small distances to occupy the new habitats and leaving their original territory unoccupied.

Additional benefits of an increase of habitat could be that an increase in habitat reduced density-dependent competition for other disturbance-dependent shore species, such as American Oystercatcher, Least Tern (*Sternula antillarum*), Killdeer (*Charadrius vociferus*) or Wilsons Plover (*Charadrius wilsonia*) (Elliot-Smith and Haig 2004). On Atlantic Coast barrier islands, American Oystercatchers nest in similar habitat to plovers, have been known to have aggressive encounters with plovers, and are suspected to have caused plover nest failure of in some cases (Hogan et al. 2018, S. Robinson, personal observation). Similarly, aggression between Wilsons Plovers and Piping Plovers is suspected to influence territory spacing in Virginia (Bergstrom and Terwilliger 1987). A reduction in interspecific competition by an increase in habitat may have allowed an increase in areas for plovers to settle in some cases, contributing to positive population growth for Piping Plovers.

Evidence of the effect of habitat change on populations of breeding plovers is commonly studied at individual breeding sites (Boettcher et al. 2007, Cohen et al. 2009, Schupp et al. 2013, Catlin et al. 2015). Plovers on the Atlantic coast are dependent on overwash from high water levels to control vegetation (Cohen et al. 2009). Plovers in riverine systems are dependent on floods occurring at relatively frequent intervals to create habitat and reduce vegetation encroachment (Zeigler et al. 2017a, Hunt et al. 2018). In many of these disturbance-dependent systems, human intervention can act as a surrogate for the natural systems by building habitat that allows the population to increase (Catlin et al. 2015). However, it may be necessary to intervene in a manner that would mimic prior disturbance regimes in order to avoid detrimental effects that may result from static habitat, such as vegetation succession. Human intervention can also increase functional habitat for plovers and other beach nesting shorebirds by protecting habitat from human use. Typically, this is in the form of restricted pedestrian and vehicle access.

Population increases following functional habitat increase are also suggestive of habitat limitation, with the increase in habitat and a decrease in functional density resulting from protection rather than creation. An example of this for plovers is in Massachusetts where the population has increased nearly 400% from 136 to 687 pairs since listing, primarily due to active human and habitat management (USFWS 2016).

Human intervention has increased available habitat and led to population increases with Little Ringed Plovers (*Charadrius dubius*), Long-billed Plovers (*Charadrius placidus*), and Piping Plovers (Parrinder 1989, Cohen et al. 2009, Katayama et al. 2010, Arlettaz et al. 2011, Catlin et al. 2015, Walker et al. 2019). On the Missouri and other prairie rivers, Westhampton Island and Assateague Island, human actions mainly acted to inhibit the natural dynamics, by building dams and channelizing the river (Cohen et al. 2009, Schupp et al. 2013, Catlin et al. 2015). The Virginia barrier islands and Cape Lookout are not managed to prevent or repair overwash, unlike many other barrier islands, which is likely why the habitat from Hurricane Isabel was created and persisted. Thus, although human intervention can create habitat for short term plover increases, natural dynamics, or repeated human interventions, are essential for habitat maintenance.

It is key that we understand what is limiting populations of imperiled species, to properly manage for population recovery. A population that is regulated by density-dependent factors also can be decreased, at least temporarily, by density-independent factors, such as storms or overharvest. Density-dependent vital rates, such as reproduction, immigration, emigration, and factors affecting them, such as predation, can be influenced by the amount of available habitat, and their impact on a population can increase or decrease with a change in habitat amount. However, if the effect of habitat limitation is not acknowledged when trying to influence such

factors, ineffective management can occur. Predation has been shown to be influential to plover success (e.g., Patterson et al. 1991, Catlin et al. 2011b, Hunt et al. 2018) and predation rates can vary with habitat, such that an increase in habitat can influence nest and chick survival by reducing detection by predators (Elliot-Smith and Haig 2004, Catlin et al. 2015, Swaisgood et al. 2017, Hunt et al. 2018). Predator populations also can be reduced by events that create habitat for piping plovers, such as hurricanes and floods, but a single reduction event may not affect prey populations for long (Stocking et al. 2017). Therefore, if predators are managed where prey are habitat-limited and the amount of habitat does not increase, the population response may be small and/or inconsistent. It can be challenging to identify the proximate causes of population change, thus additional studies of habitat, prey populations and predator populations, and their interactions would be beneficial.

Although they have experienced range-wide population increases since their listing in 1986, plovers have not reached recovery goals in most areas (USFWS 2009, 2016). With strong evidence for habitat limitation across the plover's range, creating and enhancing habitat that is also managed to avoid human disturbance and subsidized predators should allow populations to grow. For Atlantic Coast plovers, allowing overwash to occur naturally will help to restore and maintain their early successional habitat (Schupp et al. 2013). Natural overwash should be allowed, where possible, in plover nesting areas, both for the benefit of the plovers, and the barrier island, as natural inlet formation and overwash processes assist in maintaining barrier islands (Smith et al. 2008, Seavey et al. 2011). It also is possible that increased storminess from climate change (Weisse et al. 2012, Vermaire et al. 2013) could enhance plover nesting habitat on the Atlantic Coast by increasing frequency of overwash and breaches unless the islands are altered to prevent such habitat change. Barrier islands that have been engineered to prevent

overwash will likely require frequent active management to mimic the disturbance of a habitat-creating event (Elias et al. 2000, Cohen et al. 2009). For Missouri River plovers, floods such as the one that occurred in 2011 are damaging and expensive to the human infrastructure near the river (USACE 2012). Building habitat to mimic the flood-created sandbars can mitigate the successional transition of the sandbars from open sand to highly vegetated, although building rarely mimics the scale of natural creation due to expense (Hunt et al. 2018). However, habitat creation can be successful for both river and coastal plovers (Hunt et al. 2018, Cohen et al 2009). Future management for plovers range-wide should focus on increasing the amount of available habitat and restoring natural habitat disturbance regimes where possible, therefore increasing the overall carrying capacity of the plover range, and allowing populations to reach regional and range wide recovery goals.

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Tables

Table 1. Pair counts, potential nesting habitat from classified imagery and nesting density for six study areas in which we investigated piping plover irruptions following habitat-creating events.

Years shown are years that we classified imagery before and after habitat-creating events (hurricanes and floods). The year of the event is in brackets after the study area name.

Study Area	Year	# Pairs	Potential nesting habitat (ha)	Nesting density (pairs/ha)
Cape Lookout [2003]	2003	5	78.6	0.062
	2006	20	100.1	0.20
Cedar and Metompkin islands [2003]	2002	53	229.7	0.23
	2005	84	293.1	0.29
Wreck Island [2003]	2002	0	32.0	0.00
	2006	6	73.1	0.082
Gavins Point Reach (2000's) [2010, 2011]	2009	119	119.2	1.00
	2014	119	1250.9	0.095
Gavins Point Reach (1990's) [1997]	1996	11	-	-
	2000	93	-	-
Westhampton (1930's) [1938]	1937	9	-	-
	1941	65	-	-
Westhampton (1990's) [†] [1992]	1992	0	22.3	0.00
	2000	38	39.9	1.05
Assateague Island, MD [1992]	1990	14	-	-
	1997	60	-	-

[†]Estimates from Cohen et al. 2009

Figures

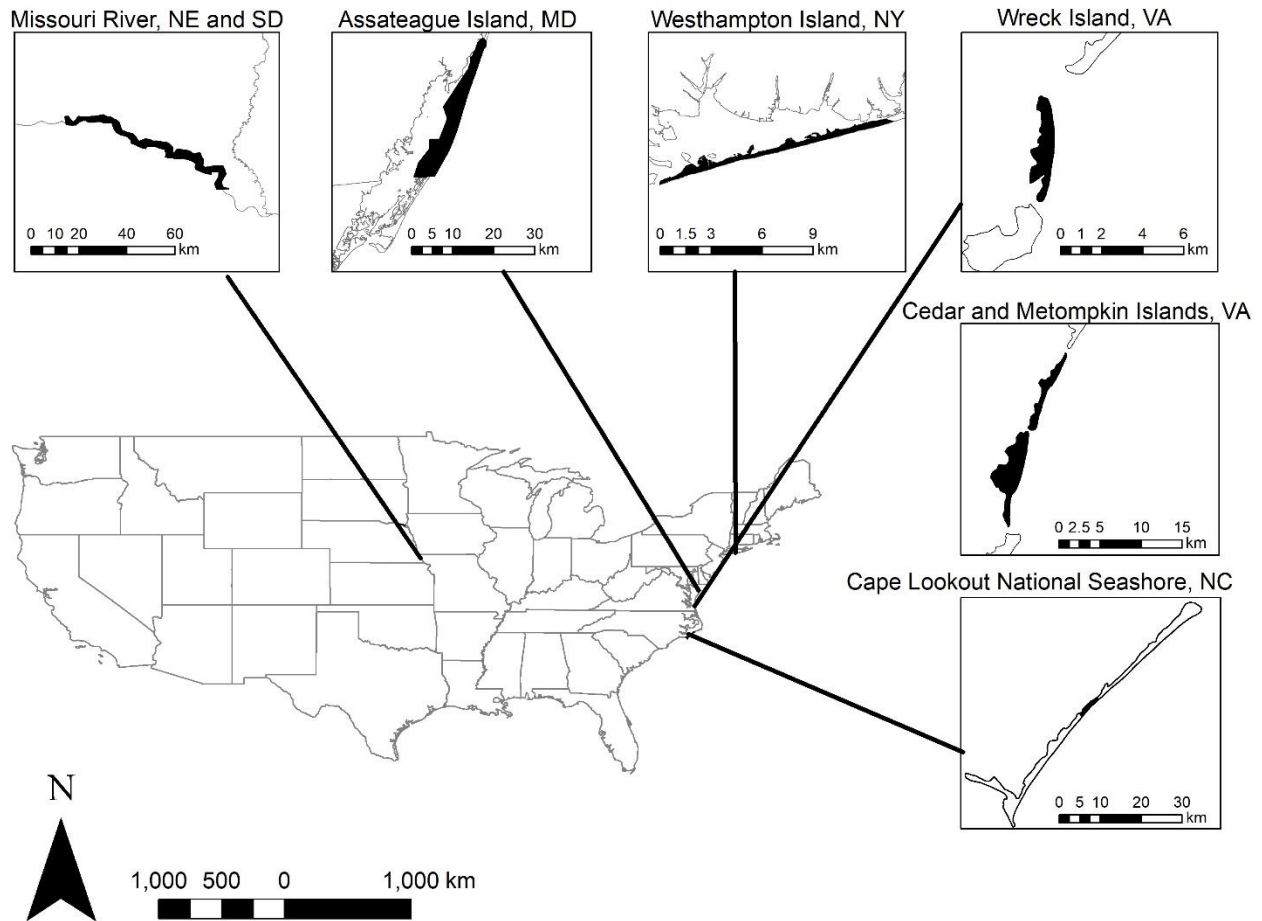


Figure 1. Study area showing six study areas, in which we investigated piping plover population irruptions following habitat-creating events. The furthest west study was on the Missouri River below the Gavins Point Dam, from 1994–2000, 2009–2015. On the Atlantic coast we had six irruption events, three on the barrier islands of Virginia (Metompkin, Cedar, and Wreck islands) from 2001–2008, one on Cape Lookout National Seashore from 2002–2008, one on Assateague Island, Maryland from 1990–1997 and two on Westhampton Island, New York, from 1937–1947 and 1992–2000.

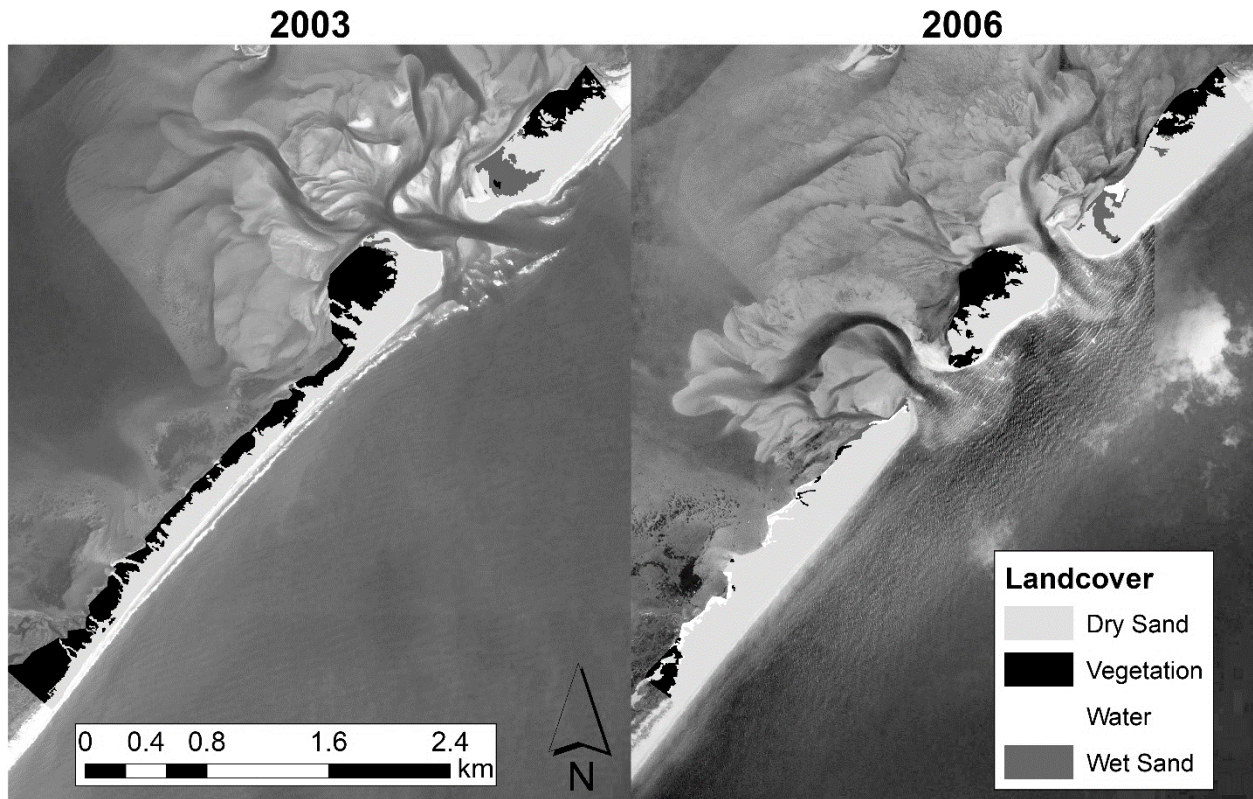


Figure 2. Cape Lookout, North Carolina around Ophelia Inlet from before Hurricane Isabel in 2003 (left) and after Hurricane Isabel in 2006 (right). Classification from eCognition overlaid on respective imagery. Hurricane Isabel occurred in the fall of 2003.

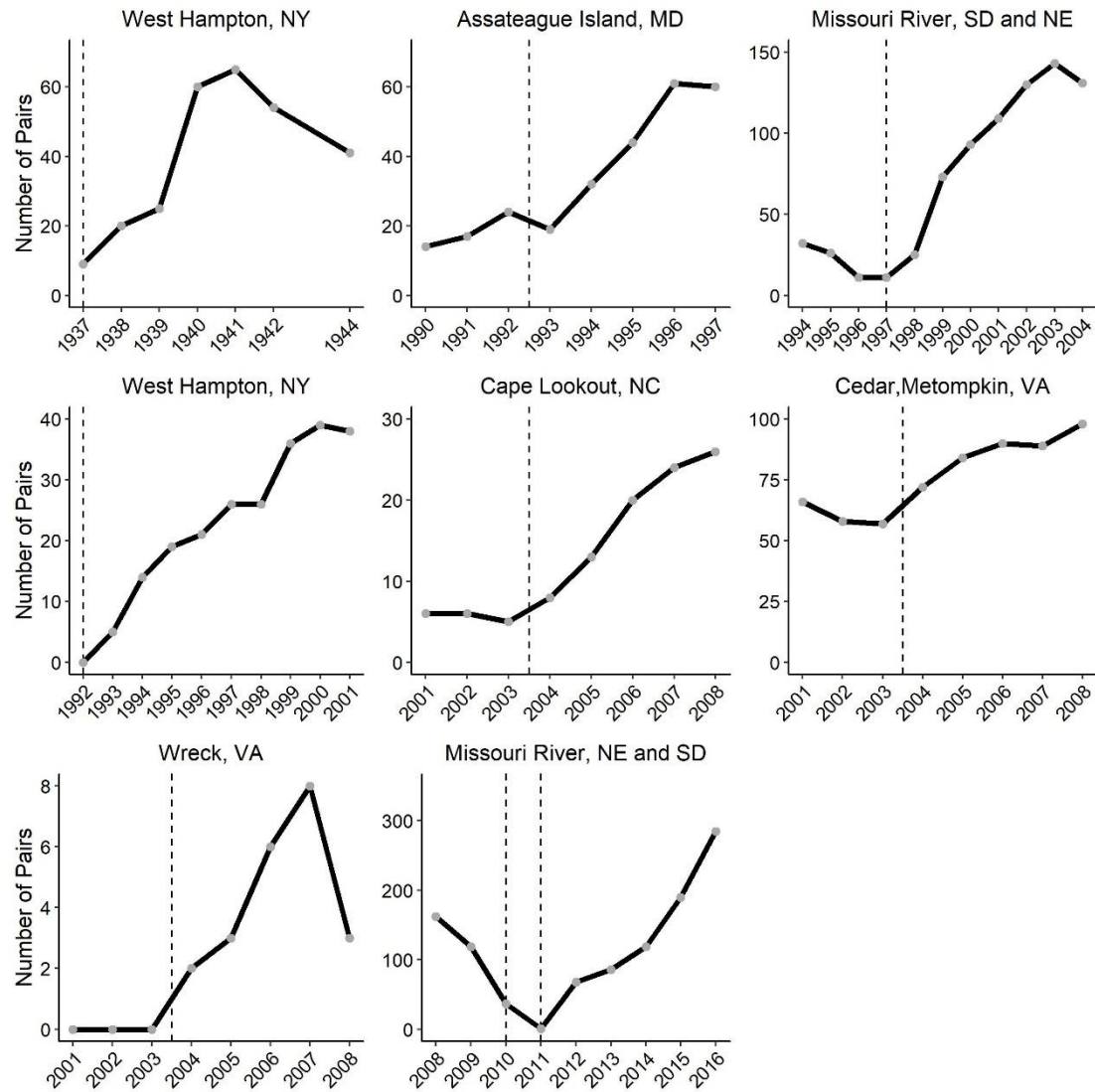


Figure 3. Pair counts for eight case studies of piping plover population irruption following habitat-creating events. Vertical dashed lines indicate timing of the habitat-creating event.

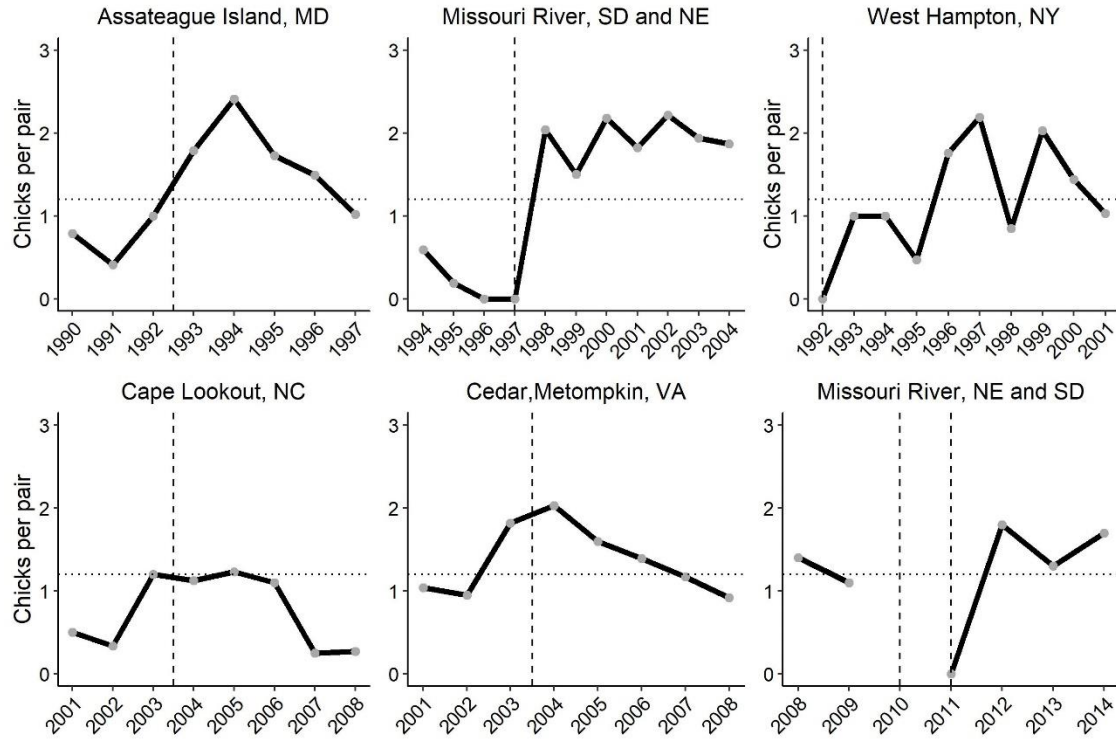


Figure 4. Productivity (chicks/pair) for six irruption case studies following disturbance creating events. The horizontal dotted line represents the estimated reproductive output required for stationarity (1.2 chicks/pair). Vertical dashed lines indicate approximate timing of the

disturbance creating events. Productivity data is missing from the Missouri River in 2010 due to incomplete monitoring following high water events.

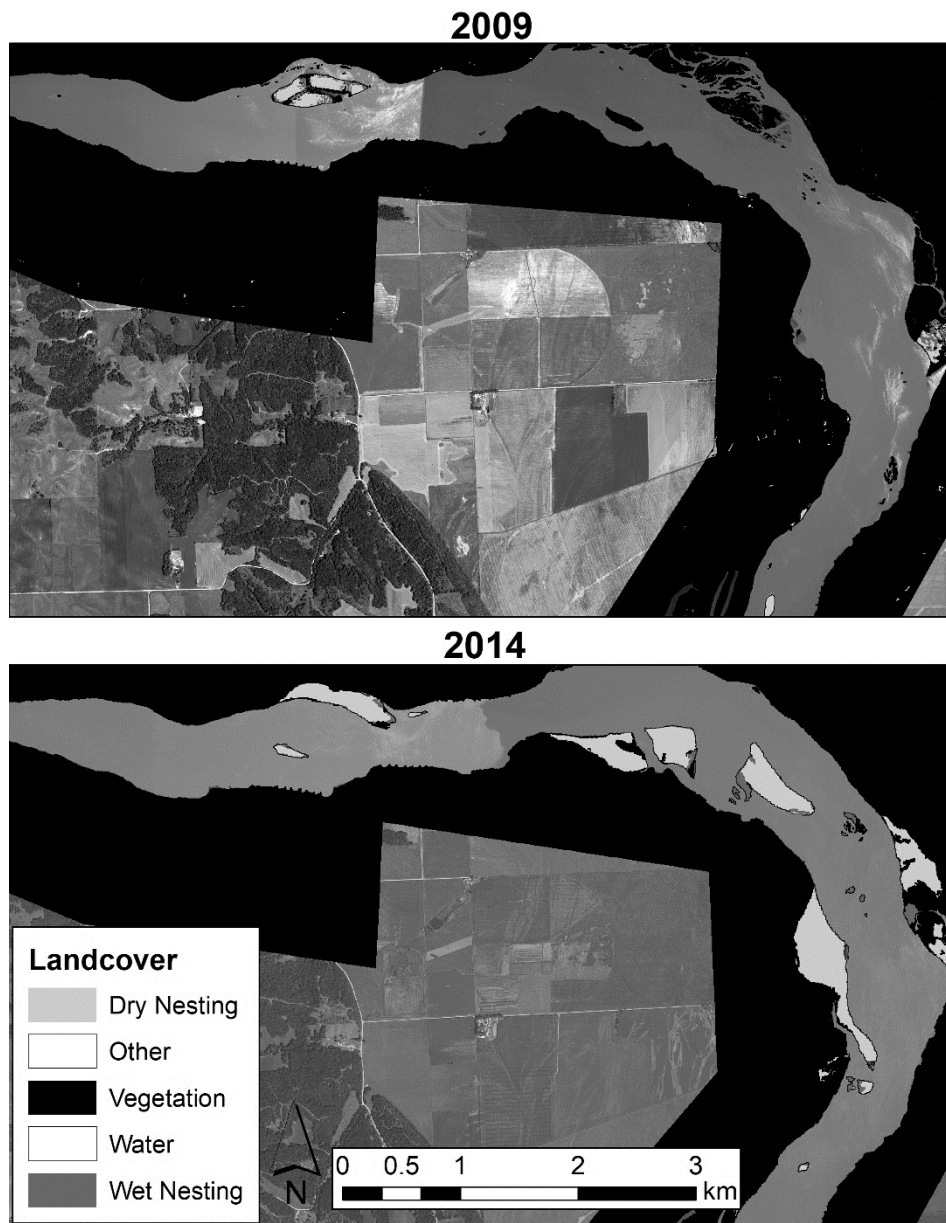


Figure 5. Portion of Missouri River classification from 2009 (top) and 2014 (bottom).

Classification from eCognition overlaid on respective imagery. The habitat class ‘other’ included

clouds, shadows and human development. High water and flooding occurred on the Missouri River in 2010 and 2011.

Appendix A. Additional classification map examples for irruption study sites

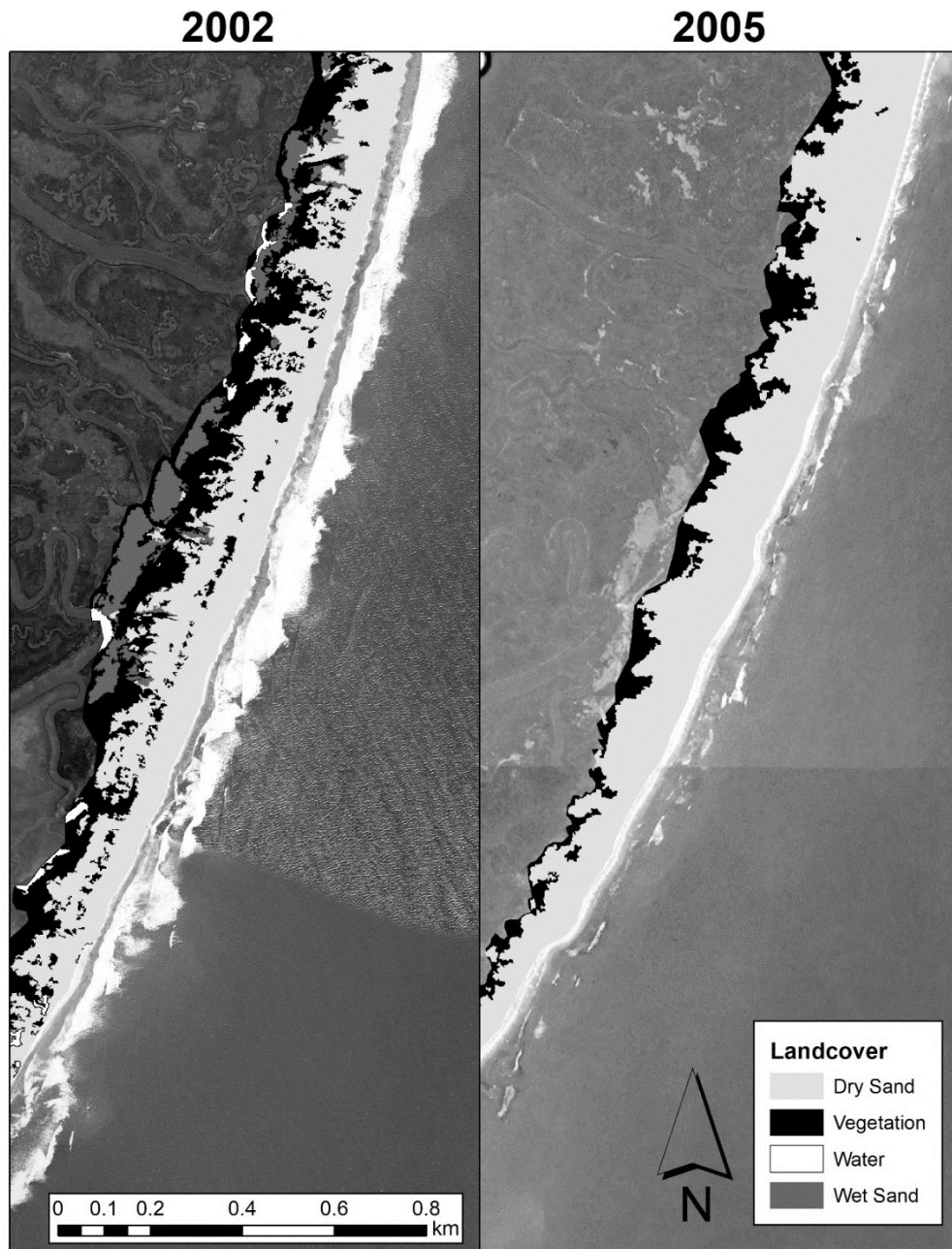


Figure A1. Portion of Cedar Island classification from before Hurricane Isabel in 2002 (left) and 2005 (right). Classification from eCognition overlaid on respective imagery. Hurricane Isabel occurred in the fall of 2003.

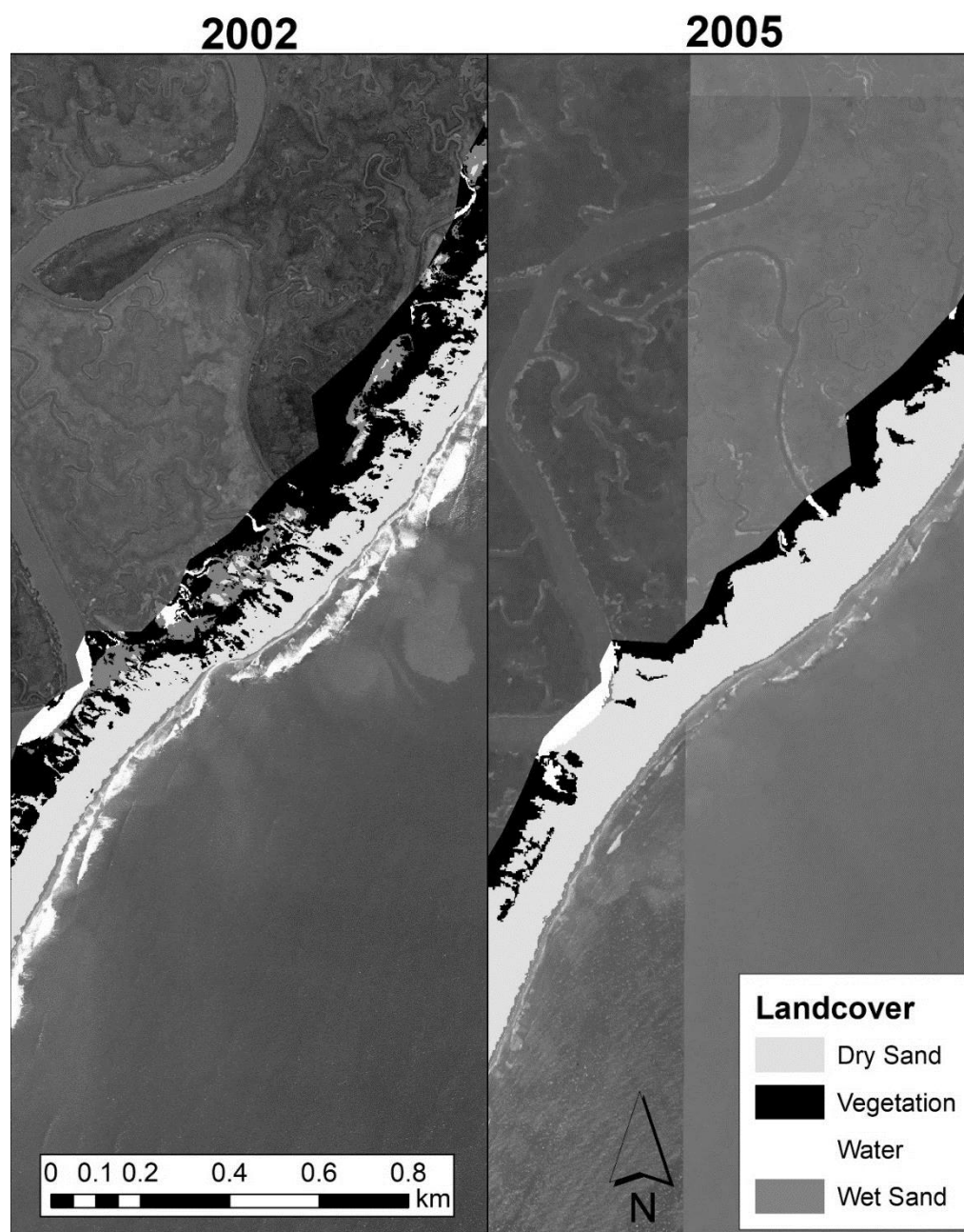


Figure A2. Portion of Metompkin Island classification from before Hurricane Isabel in 2002 (left) and 2005 (right). Classification from eCognition overlaid on respective imagery. Hurricane Isabel occurred in the fall of 2003.

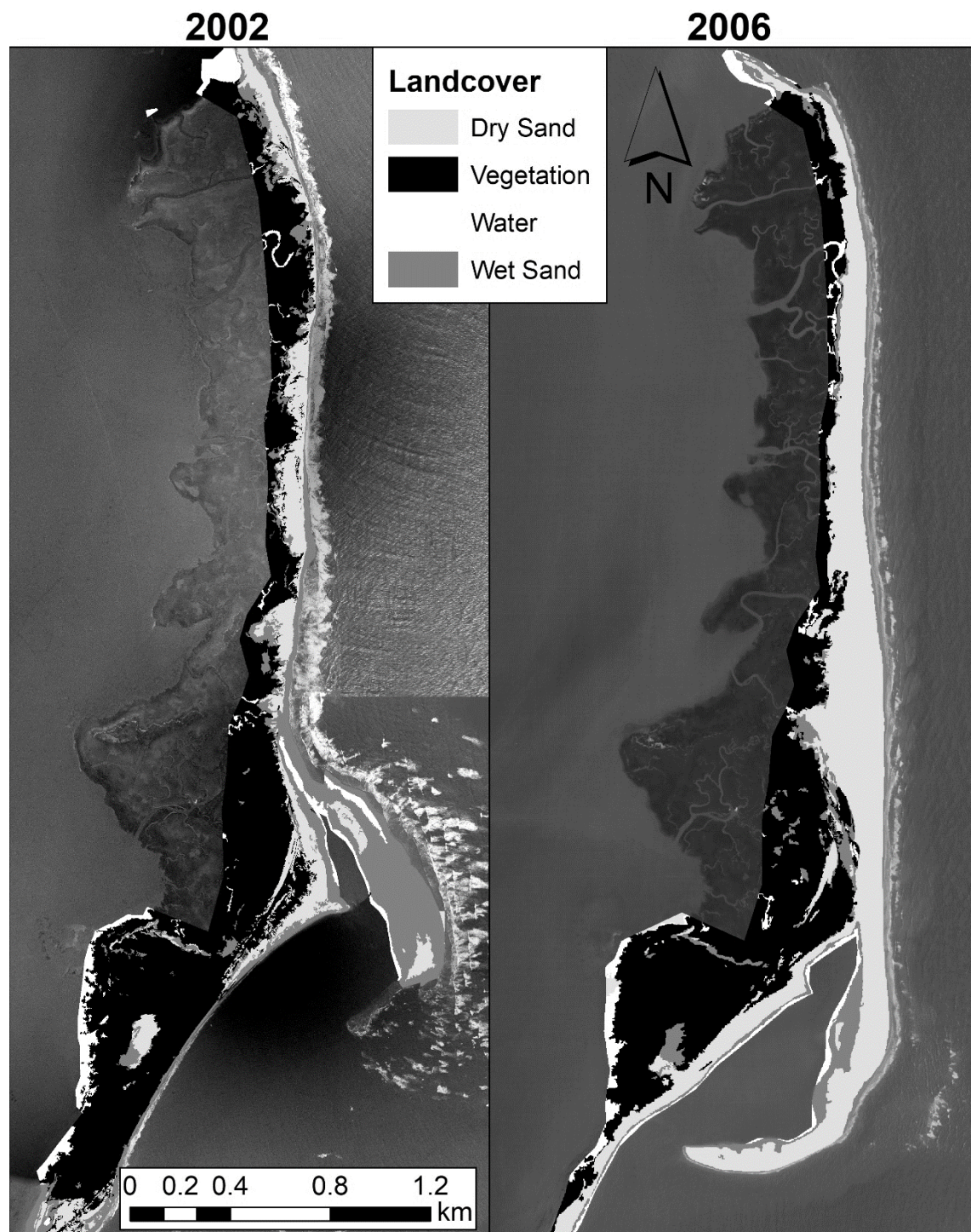


Figure A3. Figure A1.3. Wreck Island classification from before Hurricane Isabel in 2002 (left) and 2006 (right). Classification from eCognition overlaid on respective imagery. Hurricane Isabel occurred in the fall of 2003.

**CHAPTER 2. PIPING PLOVER POPULATION CHANGE IN A HURRICANE AFFECTED POPULATION
AND THE RELATION TO CONSTRUCTED NESTING HABITAT**

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Piping plover population change in a hurricane affected population and the relation to
constructed nesting habitat

Samantha G. Robinson^{1,*}, Daniel Gibson¹, Thomas V. Riecke², James D. Fraser¹, Henrietta A.
Bellman^{1a}, Audrey DeRose-Wilson^{1b}, Sarah M. Karpanty¹, Katie M. Walker¹, and Daniel H.
Catlin¹

¹ Department of Fish and Wildlife Conservation, Virginia Tech, Blacksburg, Virginia

² Department of Natural Resources and Environmental Science, University of Nevada, Reno,
Nevada

^a Delaware Division of Fish & Wildlife, Smyrna, Delaware, USA

^b Florida Fish and Wildlife Conservation Commission, Florida, USA

*Corresponding author: samgr@vt.edu

Abstract

Understanding the effects of large-scale disturbances and associated management actions
increases conservation efficacy. In October 2012, Hurricane Sandy storm surges cleared
vegetation and opened old and new inlets through, Fire Island, New York, a barrier island,
creating Piping Plover (*Charadrius melodus*; plover) habitat. Storm effects prompted an island-

wide stabilization project, which could negatively affect novel and existing plover habitat. Certain sections of Fire Island were designed to create and/or improve plover habitat (hereafter, restoration areas) to mitigate possible habitat loss or degradation. Since plovers in New York appear to be habitat-limited, we anticipated positive population growth following habitat creation. We developed an integrated population model to assess the effect of Hurricane Sandy created habitat, and restoration areas on demographic processes during 2013–2018. We observed positive population growth in three of five years, and overall growth through the period ($\bar{\lambda}$ = 1.12). Immigration and reproductive output were correlated with population growth ($r = 0.93$, and 0.74 , respectively). Compared to the rest of the study area, restoration areas had higher chick survival and lower nest survival and site fidelity. The result was population growth ($\bar{\lambda}$ = 1.09) in restoration areas, similar to the whole study area. Restoration areas contributed ~7% of the natal recruits breeding in the population and ~8% of the adults remaining in the population, similar to what could be expected based on proportional island shorefront (~7%). In the short term, restoration areas seemed to mimic natural plover habitat. Vegetation removal, an important process in renewing natural plover habitat, likely will be necessary to maintain habitat suitability, especially as restoration areas age. Efforts to increase immigration of novel breeding adults into the system, primarily by habitat creation or maintenance, is likely to have the greatest local effect on population growth. Management to improve reproductive output is likely to have a positive effect on population growth if there is suitable habitat to support recruits.

Keywords: barrier islands, *Charadrius melodus*, endangered species, habitat creation, Hurricane Sandy, integrated population model

Introduction

Understanding the contribution of each demographic parameter to population change, particularly in the face of changing environments, is essential for knowing where and how to focus ever-dwindling conservation resources. Population change is an outcome of numerous, often correlated, demographic processes that respond to various environmental stimuli (Newton 1998). Most commonly, strategies focus on a single demographic parameter (e.g. nest success, adult survival, reproductive output, etc.; Botkin and Miller 1974, Martin 1988, Annett and Pierotti 1999). However, estimating population parameters separately makes it challenging to compare and understand relative contributions to population change of individual parameters (Schaub and Abadi 2011). Thus, analytical approaches that consider multiple demographic inputs into population growth allow for a more holistic assessment of how a species responds to environmental variation, and allows for efficient targeting of conservation funding towards the specific vital rate(s) contributing the most to population change.

Changes in local population size can result from fine-scale effects, such as area-restricted habitat change or management, or regional changes, which can be detected through population synchrony or correlated changes in multiple populations (Mortelliti et al. 2015). Such synchronous changes could be explained by regional climate or weather patterns, high levels of immigration and emigration, or regional synchrony in predator populations (Liebhold et al. 2004). Habitat altering disturbances, both at fine and broad scales, also can lead to population change through these mechanisms and can affect each individual demographic process. At the local scale, an increase in habitat through disturbance events, such as storms or habitat modification, can lead to a release from density-dependent processes such as crowding (Rodenhouse et al. 1997, Catlin et al. 2019). Changes in habitat amount or quality at fine scales

likewise can affect broader scales, particularly if a population is a source following disturbance (Pulliam 1988). Alternatively, disturbances can negatively affect populations, such as if a disturbance event occurred simultaneously with animal presence on the landscape and resulted in increased mortality, lowered reproductive output, or movement away from the site (Wunderle and Wiley 1996, Hunt et al. 2018).

The Piping Plover (*Charadrius melodus*; plover) occupies landscapes that are highly affected by both anthropogenic and natural disturbance at both local and regional scales. Plovers are a temperate breeding shorebird listed under the United States Endangered Species Act (1973) due to habitat loss, human disturbance, and predation (USFWS 1985). Plovers are ground nesters, preferring sparsely vegetated, dry sand (Elliot-Smith and Haig 2004), typically laying four egg clutches in scrapes in the sand, and hatching precocial young. The adults and chicks are reliant on moist or saturated shoreline for foraging habitat. Preferred sites typically have low wave energy and gradually sloping shorelines such as bayside intertidal habitats in coastal systems or backwater areas in riverine systems (Patterson et al. 1991, Elias et al. 2000, Fraser et al. 2005, Le Fer et al. 2008, DeRose-Wilson et al. 2018). Plovers arrive on the breeding grounds after mid-March, and they initiate southward migration between July and September (Elliot-Smith and Haig 2004). Throughout the range, each plover population faces unique threats and challenges to recovery, such as flow modification in the Great Plains' rivers or beach modification and human recreation on the Atlantic Coast (Catlin et al. 2015, DeRose-Wilson et al. 2018, Gibson et al. 2018, Walker et al. 2019). Plovers generally are found in systems that are sensitive to habitat altering disturbance events such as storms or floods, or disturbances that create open, sparsely vegetated sand on the breeding grounds where they often are habitat limited (Cohen et al. 2009, Catlin et al. 2015, Hunt et al. 2018, Robinson et al. 2019, Walker et al. 2019).

Storm or flood surges that bury or remove vegetation, can have positive effects on breeding plover population size (Cohen et al. 2009, Catlin et al. 2015, Gibson et al. 2018). Maintenance of plover habitat requires relatively frequent disturbance to remove vegetation or deposit sand (e.g., approx. 4 years on the Missouri River; Zeigler et al. 2017). However, human intervention has modified the frequency of possible disturbance through the disruption of natural processes (Catlin et al. 2015, Walker et al. 2019). Furthermore, human use of the shoreline further reduces functionally available habitat for plovers (Maslo et al. 2018, 2019; Walker et al. 2019) and can have negative effects on specific vital rates such as adult and chick survival (DeRose-Wilson et al. 2018, Gibson et al. 2018).

In October 2012, Hurricane Sandy intersected the Atlantic Coast, causing widespread damage to infrastructure and extensive sand movement in beach systems (Smallegan et al. 2016). Two barrier islands and plover nesting sites in New York, Fire Island and Westhampton Island, experienced considerable movements of sand and ocean water across the islands, forming several areas of open dry sand extending from ocean beach to bay shorelines. Barrier islands are narrow, low-lying, strips of sand that lie parallel to the mainland in some coastal systems (Leatherman 1988). Three breaches in the islands (i.e., areas where the ocean water was able to connect and flow continuously to the bay) also resulted from the storm (Hapke et al. 2013). The United States Army Corps of Engineers (USACE) subsequently filled two of the breaches (USFWS 2014, Walker et al. 2019). Due to concerns about the ability of the island to protect mainland Long Island from future storm impacts, the Fire Island to Moriches Inlet Stabilization (FIMI) project was initiated to prevent future overwashes (USACE 2014). The project involved the creation of dunes, which were stabilized by planting American beach grass (*Ammophila breviligulata*). However, the stabilization project had the potential to negate some of the positive demographic

effects for plovers of Hurricane Sandy by interrupting nesting areas of flat, sparsely vegetated dry sand and plover access to bay side low-energy intertidal habitats. The United States Fish and Wildlife Service (USFWS) wrote a biological opinion following a biological assessment of the stabilization project to determine whether the project had the potential to jeopardize the continued existence of breeding plovers (USFWS 2014). As a result of the biological opinion, two mitigation areas on the island were built to create plover nesting habitat (hereafter; restoration areas; Bellman 2018, Walker et al. 2019, Zeigler et al. 2019). Following conservation initiatives such as habitat restoration, it is helpful to understand how those actions influence the population to inform future management or conservation actions (Stem et al. 2005, Catlin et al. 2011).

Plover dispersal has been documented among management and recovery units (Haig and Oring 1988a, Cohen et al. 2009, Hillman et al. 2012, Amirault-Langlais et al. 2014, Catlin et al. 2016). This observed dispersal suggests that emigration and immigration are influential to plover population dynamics at both local and regional scales, thus, there is interest in understanding site-specific population drivers. Models that explicitly incorporate immigration and emigration can be used to estimate site-specific vital rates, to understand the relationship of those rates to population change, and to evaluate the effects of disturbance or specific management actions. While these estimates are important, model-based estimates of immigration and emigration are influenced by an observer's definition of a study system and therefore have a mixture of biological and human-derived constraints, and care should be taken interpreting them and comparing among explicit values.

Past studies of plovers have found that population growth varies with density (Cohen et al. 2009, Hunt et al. 2018), habitat type (Catlin et al. 2015). Moreover, population growth may

vary substantially across geographic locations (Calvert et al. 2006, Weithman et al. 2019).

Plovers are habitat limited across much of their range, and thus, we hypothesized that an increase in nesting habitat, both from Hurricane Sandy and the creation of the restoration areas, should lead to an increase in the population size (Robinson et al. 2019). We were interested in quantifying both the population change of a small, hurricane-affected plover population in New York and understanding the relationship of USACE-built habitat to annual population growth through reproductive output and site fidelity. Our objectives were 1) to determine how various demographic rates (i.e., chick survival, nest survival, immigration) contributed to population change on Fire and Westhampton islands (hereafter; Fire Island) and 2) to evaluate the effect of plover habitat built by the USACE on demographic rates and overall population change at this site and in the context of the regional population.

Methods

Study Area

We studied plovers on a 27-km stretch of Fire Island and Westhampton Island, during April to August, 2013–2018 (Figure 1). The study area consisted of Fire Island National Seashore, managed by the National Park Service, Smith Point and Cupsogue Beach County Parks, managed by Suffolk County Parks, and Robert Moses State Park, managed by New York Parks, Recreation, and Historic Preservation. Fire and Westhampton Islands have the Atlantic Ocean to the south, and several bays to the north (Figure 1). Habitat types in the study area consisted of ocean-front sandy beaches, dunes, overwashes (areas where storm water carried sand landward over the island), bay-side sandy beaches, ephemeral pools, and filled island breaches originally formed by Hurricane Sandy (Walker et al. 2019). The study area also included three inlets, Fire Island Inlet, Old Inlet and Moriches Inlet. Old Inlet was formed by Hurricane Sandy and left

open, and Fire and Moriches inlets are dredged inlets, stabilized with jetties to the east and west. Human use was variable among the management areas and comprised pedestrian and off-road vehicle use on various portions of the beach with boat access along the bay-side shore line (DeRose-Wilson et al. 2018).

Potential plover predators in the study area include red fox (*Vulpes vulpes*), domestic cat (*Felis catus*), raccoon (*Procyon lotor*), Common Raven (*Corvus corax*), American Crow (*C. brachyrhynchos*), Peregrine Falcon (*Falco peregrinus*), Merlin (*F. columbarius*), Great Black-Backed Gull (*Larus marinus*), Herring Gull (*L. argentatus*), and Atlantic ghost crab (*Ocypode quadrata*). Early in the study there were high densities of red fox in the study area, however mange outbreaks occurred in 2015 and 2017, significantly reducing the local red fox densities (Robertson et al. 2019).

The USACE created two restoration areas on Fire Island between the 2014 and 2015 plover breeding seasons (Figure 2). The restoration areas were designed to mimic natural plover habitat and were created to mitigate for the potential loss of plover habitat caused by the FIMI. The Great Gun restoration area nominally was 34.8ha, approximately 1500m long and 160m wide, and was constructed by flattening topography, removing vegetation and sand from some areas, and adding sand in other areas. The New Made restoration area was 6.6ha, approximately 375m long and 240m wide, and was originally a deposit site for dredged material. New Made was constructed by flattening, and removing and burying vegetation with added sand (USFWS 2014, Bellman 2018). Since the creation of the restoration areas, the response to vegetation succession has been different between the two sites with revegetation occurring more rapidly at New Made than Great Gun (Bellman 2018, S. Ritter unpublished data). New Made restoration area, in addition to being smaller, was situated north of a sand road and had little to no access to

bayside foraging habitat once vegetation succession, primarily in the form of phragmites began. Great Gun restoration area, alternatively, had ample access to ocean intertidal foraging habitat and the associated wrack.

Field Methods

We surveyed for adult plovers beginning in the spring of each year (range: April 1–May 14), concluding in the late summer of each year (range: August 23–September 26). We surveyed areas every two to three days using linear transects approximately 100–300m apart. We resighted banded or flagged birds using 20–60x spotting scopes. While surveying for adults, we searched for nests by closely watching the ground and by observing adult behavior. When a nest was found, we collected the location using a Garmin (Garmin International, Olathe, KS, USA) or Trimble GPS unit (Trimble Inc., Sunnyvale, CA, USA). If a nest was found with fewer than four eggs, we back-dated to an estimated initiation date assuming 1.5 days to lay each egg (Wilcox 1959, Haig and Oring 1988b). If a nest was found with four eggs or it did not increase to four eggs after four days, we floated eggs to estimate the initiation date (Westerskov 1950). We monitored all nests every one to three days until they hatched or failed, and classed nests that hatched $\geq$ one chick “successful.”

We trapped adults on nests using walk-in drop traps (Wilcox 1959) and banded adults using either a uniquely coded, field-readable UV-stable Darvic flag or a unique combination of four color bands on the tibiotarsus (2013 only). We associated adult plovers with a nest either by confirming incubation of banded birds using a spotting scope or by catching the adult on the nest. If eggs hatched, we banded all chicks as soon as possible after hatch (age range: 0–13 days), following the same banding scheme as adults. We conducted brood surveys for each brood every one to three days until chicks reached 30 days old. We considered a bird fledged at 25 days

post-hatch for consistency with past plover studies (Hunt et al. 2013, Catlin et al. 2015). We also collected auxiliary resightings of banded plovers outside of our study area but within the Atlantic Coast breeding range (North Carolina to Atlantic Canada; Catlin et al. 2015).

Integrated Population Model

As population growth is the outcome of multiple non-independent demographic processes, population models that incorporate information from interconnected demographic processes often allow for more robust inference about the importance of particular vital rates to population growth (Schaub and Abadi 2011). Here, we developed an integrated population model (IPM), which explicitly integrated population growth, nest survival, chick survival, and adult survival (Figure 3). Our IPM was based on a two-stage matrix population model; the two stages were birds from hatch to their first breeding season (SY) and after second-year birds (ASY, ≥ 1 year post-hatch). Stage nomenclature is associated with age of breeding individuals, but demographic parameters apply to the time step prior to the breeding season. Throughout, we refer to true survival, which is apparent survival corrected for birds permanently emigrating from the study site (Sandercock 2006).

Population Size. We used a hierarchical, state-space model to estimate breeding population size for each year. Plovers are socially monogamous (Catlin et al. 2015, Friedrich et al. 2015, Eberhart-Phillips 2019), so the number of pairs in a given year suggests twice that number of breeding individuals. Therefore, the data input for breeding population size was twice our estimated annual pair counts, and we estimated pair counts from known banded individuals. Because males are the primary territory holders and are less likely to move within years, if a pair divorced in a given year and the male re-mated, we counted that as the same pair. If the female re-mated, we counted that as a separate pair if it was the male's first nest (Haig and Oring

1988b). For unbanded pairs or early failing nests, we used nest proximity and initiation and failure dates to determine whether a nest could belong to an existing pair (Walker et al. 2019). We set the first population count in 2013 to 64 individuals, from our pair count of 32, due to lack of information regarding the population structure prior to the start of our study. Our state space model estimated the number of second year plovers (SY; first breeding season) and after second year plovers (ASY; 2+ breeding seasons), using stage-specific survival estimates and estimates of either the number of fledglings in the year prior or the total number of breeding adults in the year prior, respectively. The immigration component (N_{Imm}), modeled as a latent parameter representing the true process of immigration into the breeding population and an unknown amount of sampling error (Riecke et al. 2019), was estimated from a Poisson distribution with a mean value, ω . $N_{tot,t}$ is the number of individuals in year t and is composed of ASY individuals (N_{ASY}), SY individuals (N_{SY}) and immigrants (N_{Imm}), with $\tau_{N_{tot}}$ representing the observation error. $S_{Age,t-1}$ is the stage specific survival probability, $F_{Age,t-1}$ is a product of site fidelity and breeding propensity, and $Fledglings_{t-1}$ is the estimated number of fledglings produced in the previous year, $t-1$. We used the following equations to estimate the number of birds in each year, t .

$$N_{tot,t} = Normal(N_{ASY,t} + N_{SY,t} + N_{Imm,t}, \tau_{N_{tot}})$$

$$N_{SY,t} \sim binomial(S_{j,t-1} * F_{j,t-1}, Fledglings_{t-1})$$

$$N_{ASY,t} \sim binomial(S_{a,t-1} * F_{a,t-1}, N_{tot,t-1})$$

$$N_{Imm,t} \sim Poisson(\omega_{t-1})$$

Model specifications for S , F and $Fledglings$ parameters are in the following sections.

Adult Survival. To estimate adult survival rates, we developed an age-specific Barker model (Barker 1997) modified from Riecke et al. (in prep), which allowed for independent

estimates of age-specific true survival and site fidelity in a Bayesian framework. The age-specific Barker model was represented by a multistate model with six states, which jointly described the state process transition model Eq. (1) and state observation model Eq. (2). Here, the states represent 1) juveniles (local individuals captured as chicks on their natal habitat during occasion t); 2) breeding individuals (adults available for detection on the breeding grounds during occasion t); 3) emigrants (adults that have permanently left the breeding population between occasions $t-1$ and t); 4) harvested or recovered individuals (individuals that were recovered and reported dead between occasions $t-1$ and t); 5) undetected mortality (individuals that died or were harvested and not recovered/reported between occasions $t-1$ and t); and 6) final or absorbing death (died prior to occasion t).

$$\psi_{i,t} = \begin{bmatrix} 0 & S_j F_j & TS_j(1 - F_j) & 0 & 0 & (1 - S_j) \\ 0 & S_a F_a & TS_a(1 - F_a) & (1 - S_a)rf & (1 - S_a)R'(1 - r) & (1 - S_a)(1 - R')(1 - r) - f \\ 0 & 0 & S_a & (1 - S_a)rf & (1 - S_a)R'(1 - r)(1 - S_j)R' & (1 - S_a)(1 - R')(1 - r)(1 - S_j)(1 - R') - f \\ 0 & 0 & 0 & 0 & 0 & 1 \\ 0 & 0 & 0 & 0 & 0 & 1 \\ 0 & 0 & 0 & 0 & 0 & 1 \end{bmatrix} \quad (1)$$

Two states were partially observable, breeding and emigrating Eq. (1). True survival is represented by S_j and S_a , and breeding fidelity is represented by F_j and F_a for SY and ASY birds, respectively. Our design also represented several detection parameters. Detection of individuals within the spatial confines of the study system as breeders is represented by p whereas detections of individuals outside of the study system are represented by R . Within a year, both breeding individuals and emigrants can be seen within and outside the study system, but breeding individuals must have been confirmed incubating a nest or brooding chicks. The probability of being resighted during an off-site period, given a bird died in that period is R' .

Finally, the model contains a recovery parameter (f). Plovers are not harvested and band recoveries from individuals within our study system are extremely rare, thus, we fixed f to zero Eq. (1), but describe the full model to allow for broader use in other systems.

$$\Omega_{i,t} = \begin{bmatrix} 0 & 0 & 0 & 0 & 1 & 0 \\ 0 & pR & p(1-R) & (1-p)R & (1-p)(1-R) & 0 \\ 0 & 0 & 0 & R & (1-R) & 0 \\ 0 & 0 & 0 & 0 & 0 & 1 \\ 0 & 0 & 0 & 1 & 0 & 0 \\ 0 & 0 & 0 & 0 & 1 & 0 \end{bmatrix} \quad (2)$$

In Barker models, entry into the study system is conditioned on first capture. Therefore, transitions to the juvenile state, as well as juvenile detection are implicit, and estimation of these parameters is not needed. Similarly, because primary occasions in our application of the model represent breeding seasons, juveniles that survive the winter must transition into adulthood (i.e., breeders or emigrants) and cannot remain as juveniles. For this model, entry into the 1st age class was conditioned on a chick fledging, and transitions into the 2nd age class occurred during the nesting period of each breeding season. Thus, the survival period for SY was from fledging to following nesting season (approx. 8 months), whereas, the survival period for ASY represented the entire year between nesting periods.

We defined ‘on-site’ as an individual that was confirmed nesting in a given year. Because site-faithful individuals all were confirmed as breeders, our estimate of fidelity also incorporated breeding propensity, which otherwise would need to be estimated in the population model (Weithman et al. 2017, Catlin et al. 2019). We defined ‘off-site’ as all individuals that were hatched from, or at one time nested in our study area that were seen anywhere on the Atlantic plover breeding grounds (North Carolina to Atlantic Canada) during the breeding season (April to September).

We did not allow either of the detection parameters (i.e., p , R) to vary by year or age to reduce model complexity and based on evidence from past estimation of these rates in another study (Weithman et al. 2019). We modeled hatch-year and adult survival and fledging as varying by stage, but not year. We did not include individuals captured in the final year of the study (2018) in encounter histories.

Nest Survival. For nest survival we used the following logistic exposure model (Eq. 3; Rotella et al. 2004, Shaffer 2004, Kozma et al. 2017) to estimate daily nest survival.

$$DSR_i = \frac{e^{\beta_0 + \sum_j \beta_j x_{ji}}}{1 + e^{\beta_0 + \sum_j \beta_j x_{ji}}} \quad (3)$$

In this model, i represents a day, j represents covariates and β_j the coefficient of covariate j (Rotella et al. 2004). We then raised the daily survival rate to the 34th power to estimate probability of surviving to hatch (*Annual. Nest*). We used 34 days as it is the average time from the first laid egg to hatch in plover nests (Catlin et al. 2015). We included a fixed effect of year as Fire Island nest survival has been shown to vary by year (Weithman et al. 2019). We also calculated the mean clutch size of successful nests (*Mean. Clutch*), using only clutches that reached a complete clutch, which we defined as at least four nest visits (approximately 8 days) with the same egg count.

Pre-fledging chick survival. We estimated chick survival with an adaptation of the Dail-Madsen model, a dynamic N-mixture model, which was originally developed to estimate abundance in open populations (Dail and Madsen 2011). Our adaptation of the model is analogous to the young survival model that has historically been implemented in program Mark (Lukacs et al. 2004), but for a Bayesian framework. The Lukacs model has several assumptions that must be met, and our primary concern was the assumption of no movement between broods, which has been observed in our study (Weithman et al. 2019). Brood mixture, if substantial and

unaccounted for, can lead to bias in traditional young survival models (Lukacs et al. 2004). To account for undetected between-brood movement, we included an immigration term to represent undetected mixing among broods. This model assumes that brood immigration is random and probability of entering a brood is identical to the probability of leaving a brood. Each encounter history was brood-specific and represents the maximum chick count over a 5-day encounter occasion. The resulting estimate from the model is the probability of a single chick surviving each five-day interval. We then took the product of the five-day intervals as the probability of surviving to fledge, or 25 days (*Annual.Chick*). We constrained $N_{chick,j,1}$ to be a known quantity, which assumed that we knew how many chicks hatched from a brood either by catching them all in the nest bowl or by observing how many eggs were left in the nest at termination (Eq. 4). Most plover nests (90%) in our study that hatched had been protected from many predators by encircling with wire fencing topped with blueberry netting (exclosed), so there was little opportunity for partial clutch depredation. The number of individuals in subsequent periods ($N_{chick,t+1}$) was the sum of the number of individuals that survived and were observed from the previous period ($C_{j,t}$) and the change in the number of individuals observed between periods ($G_{j,t}$; Eq. 5). The model also produced an estimate of the number of chicks alive at any given time, $y_{j,t}$, which is drawn from a binomial distribution with a mean of the expected number of chicks ($N.chick_{j,t}$) and the detection probability (*count.p*).

$$N_{chick,j,1} = y_{j,1} \quad (4)$$

$$y_{j,t} \sim \text{binomial}(\text{count.p}_{t-1}, N_{chick,j,t})$$

$$N_{chick,j,t} = C_{j,t} + G_{j,t} \quad (5)$$

$$C_{j,t} \sim \text{binomial}((1 - \beta_{immigration}) \times \phi_{j,t}, N_{chick,j,t})$$

$$G_{j,t} \sim \text{Poisson}(\beta_{\text{immigration}} \times N_{\text{chick},j,t})$$

We then used the logit of $\phi_{w,v}$ to include fixed effects of year and occasion, where $\phi_{w,v}$ is the probability of survival for brood w at occasion v , the $\beta_{w,v}$ are brood, year or occasion specific fixed effects (Eq. 6).

$$\text{Logit}(\phi_{w,v}) = \text{mean.phi} + \beta_{t,w,v} x_{t,w,v} \quad (6)$$

Reproductive Output. We estimated annual reproductive output as the product of chick survival to fledge from the Dail-Madsen (2011) model (*Annual.Chick*), nest survival to (*Annual.Nest*) to hatch from the logistic exposure model, and the average clutch size (*Mean.Clutch*; Eq. 7). The number of fledglings (*Fledglings_t*) then was drawn from a Poisson distribution, with a mean of the number of individuals in the population (*Ntot_t*), multiplied by 0.5 and reproductive output (*Ro_t*). We multiplied the number of individuals by 0.5 as we were estimating population size in the state-space model, but reproductive output was on a per-pair basis.

$$Ro_t = \text{Mean.Clutch} \times \text{Annual.Chick} \times \text{Annual.Nest} \quad (7)$$

$$Fledglings_t \sim \text{Poisson}(Ntot_t \times 0.5 \times Ro_t)$$

Immigration, Emigration, and Lambda. We estimated the number of emigrants of each class, using the number of individuals in the year prior, age specific survival, and age specific fidelity estimates (Eq. 8, 9).

$$\text{Emigrant}_{ASY,t} = Ntot_{t-1} \times S_{ASY,t-1} \times (1 - F_{ASY,t-1}) \quad (8)$$

$$\text{Emigrant}_{SY,t} = Fledglings_{t-1} \times S_{SY,t-1} \times (1 - F_{SY,t-1}) \quad (9)$$

We estimated annual immigration rate (Eq. 10) and natal recruitment rates (Eq. 11), using the total number of individuals in the year prior and the current year's estimated number of immigrants or number of natal recruits, respectively.

$$\text{Immigration Rate}_t = N_{imm,t}/NTot_{t-1} \quad (10)$$

$$\text{Natal Recruitment Rate}_t = N_{SY,t}/NTot_{t-1} \quad (11)$$

We estimated population growth rate from one year to the next (λ) by summing the number of adults surviving from the year prior, the number of natal recruits that had returned to breed in that year, and the number of adult immigrants, dividing the number of individuals in year t by the number of individuals in year $t-1$ (Eq. 12). We also calculated the geometric mean of population growth for the entire study length.

$$\lambda_t = \frac{Ntot_t}{Ntot_{t-1}} \quad (12)$$

To understand which parameter contributed most to population change, we calculated the correlations between estimated annual population growth rate and chick survival, nest survival, reproductive output, and immigration. We evaluated the posterior mean, credible intervals, and the probability that the correlation would be different from zero to assess each value's contribution to population change. While the datasets within our IPM are inherently linked as our model and datasets are based on a closely monitored subset of the total Atlantic Coast population, a past study determined that there is little bias in using highly dependent datasets (Abadi et al. 2010).

Incorporating Restoration Areas. To estimate the effect of the restoration areas on annual population change, we incorporated the restoration areas into models through fixed effects (whether an individual or nest was associated with a restoration area) on nest survival, chick survival, and breeding fidelity. Each model had a single parameter estimate for the effect

of restoration area. We considered a nest or chick in a restoration area if they were within the boundaries of the created restoration areas (nest) or hatched from a restoration area (chick). For the chick and nest survival models, we included a nest-specific vector that indicated whether a nest was in a restoration area and a brood-specific vector that indicated whether a brood was in a restoration area. For adult and juvenile fidelity, we assigned adults to the restoration area group if they were confirmed as incubating a nest in a restoration area in a given year, and we assigned fledglings to the restoration area group if they hatched in a restoration area. For adult fidelity, we created an individual x year matrix that indicated whether a bird was originally hatched from or nested in a restoration area during the breeding season in a given year, for SY and ASY fidelity, respectively.

To estimate the population growth in the years when restoration areas were available (2015–2018), we estimated lambda for the number of individuals nesting in restoration areas and compared it to lambda for the number of individuals in the rest of the study area, excluding the restoration areas. We derived restoration area-specific fidelity, nest survival, and chick survival rates by using the mean estimate and adjusting for the vital rate-specific restoration area model coefficient. We also estimated the number of adults and natal recruits in year t that were from the restoration areas in year $t-1$ and what proportion of the total population they comprised to determine if the restoration areas were contributing to the whole population as would be expected based on their length relative to the study area.

All models were built and implemented in a Bayesian framework, using the *jagsUI* package to call Jags version 4.3.0 in R 3.5.2 (Kellner 2018, R Core Team 2018). We used vague priors for all estimated parameters (Supplementary Material). We assessed model fit diagnostics by visually inspecting chains and assuring convergence ($\hat{R} \leq 1.05$) was reached (Gelman and

Rubin 1992). We present estimates using the mean of the posterior distributions and the 95% Bayesian credible intervals. Model code is in supplementary material.

Results

From 2013–2018, we captured and banded 152 adult plovers and 353 chicks, and monitored 279 nests and 160 broods. Annual pairs monitored varied from 32–58 over the study period (Figure 4).

Population Change

The IPM estimated that the plover population on Fire Island increased from 64 individuals immediately following Hurricane Sandy in 2013 to 114 (CI = 83–143) individuals in 2018. These estimates correspond to what we observed in our population over the six years of the study (Figure 4). The geometric mean population growth rate for the study area ($\bar{\lambda} = 1.12$, CI = 1.05–1.17) indicated mean annual growth rates of 12%. Growth rate varied among years, and most growth occurred following 2016 (Figure 4). The population was composed primarily of adults that survived from the previous year, but there also were a substantial number of immigrants in each year (Table 1, Table 2, Figure 5). The smallest proportion of individuals consistently was natal recruits (Table 2). The immigration rate ranged from 0.40 to 0.54 immigrants per resident in $t-1$, and the natal recruitment rate was 0.05–0.26 recruits per resident in $t-1$ and was highest following years of higher reproductive output (Table 3). The number of individuals emigrating from the population to breed elsewhere varied among years. The number of breeding adults that emigrated from the population was less variable (12–17 individuals, 18.6% of adults in year $t-1$) than the number of juveniles that did not return to breed in their first breeding season (4–29 individuals, 41.4% of fledglings in year $t-1$; Figure 5).

Adult Survival and Fidelity

Mean adult true survival was 0.72 (CI = 0.64–0.79), and juvenile post-fledging true survival was similar to adult survival at 0.68 (CI = 0.57–0.81). Breeding fidelity for ASY adults was 0.74 (CI = 0.64–0.83) and 0.39 (CI = 0.29–0.51) for SY adults. The probability of detecting a living bird on the breeding grounds as a breeder in any year, given that it was present, was 0.88 (CI = 0.80–0.94).

Reproductive Output

The average clutch size was 3.84 (CI = 3.78–3.90). Nest survival and chick survival estimates had similar trends to field observations (Appendix Table 5). Nest survival varied from 0.34–0.80 (Figure 6a). Chick survival also was variable among years, 0.18–0.72, with the lowest year being the first year of the study and the highest being the final year (Figure 6b). The brood immigration parameter, which was developed to estimate undetected between-brood movement, was 0.007 (CI = 0.002–0.018), suggesting that approximately one chick out of every 143 switched broods during a 5-day time step. The first year of the study had the lowest reproductive output (0.33 chicks/pair, CI = 0.12–0.65), and the final year had the highest (1.97 chicks/pair, CI = 1.59–2.10; Figure 6c).

Correlation among Parameters

Of the parameters that contributed to population change on Fire Island, we estimated that the number of immigrants ($r = 0.93$, 0.30–0.98) and reproductive output ($r = 0.74$, -0.46–0.95) had the highest correlation with population change; 19.6% of the posterior distribution of λ 's correlation with reproductive output was less than 0, suggesting that immigration was more influential than reproductive output.

Restoration Areas

During 2015 to 2018, the restoration areas supported 3–8 pairs (8.3–13.8% of total pairs). Of all the nests monitored during these years, 29 were in restoration areas (10.4% of total nests), from which we monitored 49 chicks (13.9% of total chicks) from 14 broods (8.8% of total broods).

The mean effect of the hatching in the restoration area was negative as compared to the rest of the study area, although the credible interval incorporated zero ($\beta_{\text{nest}} = -0.65, -1.40\text{--}0.18$; Figure 7a). However, the restoration areas had higher chick survival ($\beta_{\text{chick}} = 0.78, 0.04\text{--}1.67$; Figure 7b) than the rest of the study area. The reproductive output in the restoration area was similar to the rest of the study area (Figure 7c). ASY fidelity was lower for restoration area birds ($\beta_{\text{F,ASY}} = -1.26, -2.37\text{ to }-0.072$) than the rest of the study area. There was evidence of lower SY fidelity for restoration area birds than birds in the rest of the study area but the credible interval incorporated zero ($\beta_{\text{F,SY}} = -1.11, -2.47\text{--}0.18$; Figure 7d).

The restoration areas supported an estimated 5–9% of the total natal recruits that entered the population in 2016–2018 (Figure 8), and 6–10% of the adults that survived and remained in the study area to breed in 2016–2018. The shoreline length of the restoration areas was about 7% of the total shoreline of the study area. Mean lambda for the restoration areas was 1.09 (CI = 0.90–1.30) and was equal to lambda for the rest of the study area ($\bar{\lambda} = 1.09, \text{CI} = 1.07\text{--}1.11$), although, the credible intervals around the mean population growth rate for the restoration areas overlapped one. Population growth in the restoration areas was more variable than the rest of the study area in the years following their construction (Figure 9).

Discussion

Using an integrated population model, we decomposed the demographic contributions to population change on Fire Island following Hurricane Sandy and the creation of restoration

areas. The restoration areas seemed to be retaining and recruiting the number of plovers that would be expected based on their lengths. Higher chick survival (16–46%) and lower nest survival (–9 to –44%) than the rest of the study area resulted in a reproductive output in the restoration areas that was similar to the rest of the study area. However, adults nesting in the restoration areas had a lower probability of returning to the study area. Other plover studies have reported similar trends, with plover populations responding positively to natural and artificial habitat creation in riverine (Catlin et al. 2015, Hunt et al. 2018) and barrier island systems (Boettcher et al. 2007, Cohen et al. 2009, Robinson et al. 2019).

The positive demographic trends in the restoration areas were driven by the Great Gun restoration area. This area was considerably larger than the other area, and vegetation there was removed rather than covered, slowing vegetation regrowth (Bellman 2018). The smaller restoration area, New Made, was adjacent to a marsh and quickly was overgrown by common reed (*Phragmites australis*), limiting access to foraging habitat (Zeigler et al. 2019). New Made also was narrower and located north of a road, so after foraging habitat in the area was overgrown, chicks needed to cross a sand road and two dunes to reach ocean intertidal foraging habitat. Furthermore, nesting plovers did not use New Made after the 2017 breeding season. The lower site fidelity of restoration area birds could be related to lower nest survival, but it also could be due to the proximity of the larger restoration area, Great Gun, to the eastern border of the study area. An adult from Great Gun would only need to move 2–3 km east to leave the study area, and we often found birds originally banded on Fire Island nesting in neighboring management areas. Although small sample sizes precluded assessing the two restoration areas separately, models for specific demographic parameters (i.e., nest or chick survival) can be used

in the future to understand what habitat or geographic features of the restoration areas led to higher demographic rates.

While the creation of the restoration areas in our study corresponded with the increase of the plover population, the increase also paralleled a decline in the local red fox (*Vulpes vulpes*) population during a sarcoptic mange outbreak (Robertson et al. 2019). Red foxes are known plover nest and chick predators (Ivan and Murphy 2005). The influence of foxes, and responding site-specific management, on Fire Island plovers was particularly notable in 2015 and 2018, when nesting exclosures were either omitted or removed due to foxes cuing in on exclosures. Despite the potentially lowered nest survival due to these decisions, to exclose nests or not often involves the tradeoff between adult survival and reproductive output. In other words, if exclosures increase adult predation risk, that can have a greater effect on overall population growth and persistence than the loss of a single nest (Cohen et al. 2016). The decisions to remove, or not place exclosures may have resulted in the negative mean effect of restoration areas on nest survival. Alternatively, chick survival may have been higher in the restoration areas due to lower nesting plover densities (Bellman 2018), leading to decreased intraspecific competition, or lower detection rates by predators. Studies of local predator density coupled with the effect of restoration areas may assist in distinguishing the ultimate cause of the population increase, as there may be an interaction between restoration areas and predator abundance or density.

Habitat for nesting shorebirds can be generated in a variety of ways, such as by restoring existing nesting habitat through the removal of vegetation, creating foraging habitat, and by modifying the geomorphic structure of the landscape for nesting and foraging (Powell and Collier 2000, Maslo et al. 2012, Catlin et al. 2015). Restored habitat is widely used across the

plover's range (Burger and Tsipoura 2019), and past evaluations of restoration habitat for plovers suggests they can be successful (McIntyre and Heath 2011, Maslo et al. 2012, Catlin et al. 2015). Snowy plovers (*Charadrius nivosus*) used restoration areas built for Least Terns (*Sternula antillarum*), but their nest success was low (Powell and Collier 2000). Large-scale natural processes that restore natural system function may be more effective than engineered habitat creation (Hunt et al. 2018, Walker et al. 2019).

The plover population in our study area increased over the six years of our study, as detected in our raw pair counts and the model estimates. The increase in the number of pairs following the natural disturbance of Hurricane Sandy likely resulted from localized increase in sparsely vegetated nesting habitat from storm surges overwashing previously vegetated sand and the creation of sparsely-vegetated restoration areas. Piping Plovers, like other *Charadrius* plovers (Fraser and Catlin 2019), evolved to blend in with sandy habitats to avoid detection by predators and improve survival. Thus, wide open sandy habitat assists in predator avoidance (Troschianko et al. 2016). An increase in dry sand also can increase the available habitat for birds to settle in, allowing more pairs to fit into spaces that were previously unsuitable. Both Fire Island and Westhampton Island similarly experienced an increase in access to low wave-energy moist habitats following Hurricane Sandy (Walker et al. 2019), which is selected for by plovers for higher quality forage and may have led to higher survival to fledging, reproductive output, and density (Le Fer et al. 2008).

Returning adults consistently comprised the largest part of the population, and our estimate of ASY survival was similar to survival in other breeding populations (Catlin et al. 2015, Hunt et al. 2018, Weithman et al. 2019). The consistency in adult survival rates is to be expected because during most of the year adults are spread out over the wintering areas primarily

from North Carolina and the Bahamas to Florida (Gratto-Trevor et al. 2012) and thus their survival is likely affected by average conditions over this broader area. Immigrants followed closely behind returning adults as components of the population but the variation in immigration rate was higher. Plovers are highly philopatric, so many immigrating adults likely originated in nearby populations. Because local population sizes are more likely to vary due to environmental conditions, it is to be expected that the numbers might be more variable from year to year than survival rate. Natal recruits made up a much smaller part of the population and, like immigration rate, recruitment rates were variable.

The IPM indicated that immigration was the demographic variable most highly correlated with population growth. Thus, even though the habitat was created on a local level, regional population numbers and/or reproductive output were used by this population as it responded to new habitat creation. Natal recruitment also was correlated with population growth. Thus, management for reproductive output in areas with new habitat is needed for population growth. While a habitat-based carrying capacity will determine the levels populations reach, immigration rates and reproductive rates will determine how quickly they reach carrying capacity.

The extent to which the latent parameter (i.e., immigration in this application) is fully identifiable in integrated population models is context dependent and primarily driven by violations of model assumptions (Schaub and Fletcher 2015, Riecke et al. 2019). Given our ability to effectively monitor all nesting activity, as well as mark the majority of breeding adults and nearly every chick that hatched within the study system, combined with high rates of detection of marked individuals outside the study system, it is unlikely that the immigration rates reported in this manuscript were primarily driven by other sources of model variation.

Plovers in other populations have been shown to have high site fidelity, sometimes nesting within meters of previous nesting locations (Friedrich et al. 2015), but we had a high degree of immigration ; >10 birds from each age class emigrated from our population each year. However, fidelity, immigration, and emigration rates are likely functions of the spatial scale of investigation, because we define the spatial and temporal conditions associated with the terms. Individuals that immigrated may have previously nested just outside of our small study area (Robinson et al. 2019), may have been SY individuals dispersing from their natal sites, or may have been ASY individuals dispersing from anywhere in the Atlantic breeding range. Remaining close to Fire Island, but not within the boundaries of our study site, birds may still have site fidelity to the ‘breeding population’ rather than our study area, and thus, the terminology of what is considered site-faithful is important when comparing among studies. The effect of spatial scale would be especially evident at the boundaries of our relatively small site, as a bird can become an emigrant if you just move a few hundred meters east or west out of the study area (Figure 1).

Our measure of SY survival differed from other plover survival studies that estimated true hatch-year survival (i.e., including pre-fledge chick survival; Cohen and Gratto-Trevor 2011, Catlin et al. 2015), or estimated apparent survival (product of fidelity and survival; Melvin and Gibbs 1996, Calvert et al. 2006, Catlin et al. 2014). Our estimate of true post-fledging survival was slightly higher than other studies (Catlin et al. 2015, Hunt et al. 2018, Weithman et al. 2019), and our post-fledging survival estimate was similar to our estimate of ASY survival. However, this study’s post-fledging survival estimate is only for approximately 10 months of the year, in comparison to the 12-month estimate of annual ASY survival, as post-fledging birds do not enter the system until 2–3 months into the breeding season. The similarity between estimates for the two age classes suggests that much of the risk to first-year plovers in this study occurred

prior to fledging, and first-year birds were about as likely to die as adults once they could fly. Fire Island site fidelity estimates were lower than past studies (Catlin et al. 2015), but we suspect this is because to be considered as ‘on-site’ plovers had to be confirmed breeders, therefore this estimate incorporated breeding propensity, which may not be 100% (Weithman et al. 2017, Catlin et al. 2019). Adults passed through the study area throughout the year, and some were observed on the study area but did not remain to breed. Thus, depending on how ‘on-site’ is considered, those birds, in other estimates, would be considered faithful even if they did not contribute to the breeding population. Instead, including only the birds that are known to have nested, even if some individuals are missed, focused the model on breeding birds and, in the absence of estimates of breeding propensity, likely led to a more accurate estimation of the number of individuals in each stage-class contributing to population growth, particularly immigrants.

That the population growth rate at the conclusion of our study remained positive provides evidence our population had not yet reached carrying capacity. In addition, reproductive output was higher than what would be required for stationarity in this population in four of six years (approx. 1.10 chicks/pair, Weithman et al. 2019), and we consistently had a high number of individuals immigrating into the population. Due to continued high reproductive output in 2018, the population likely will continue to increase until it reaches carrying capacity, at which time, we would expect reproductive output and/or immigration to decline due to crowding effects or site dependence (Rodenhouse et al. 1997, Catlin et al. 2015). However, there are other factors that may indicate a population is at or near carrying-capacity that we did not look into here (e.g., offspring quality, growth rates). Density-dependence is frequently cited as being influential in

breeding plover populations (Cohen et al. 2009, Hunt et al. 2018, Catlin et al. 2019), so these will be important dynamics to investigate in the future.

Coincident with the 90% increase on Fire Island, the remainder of the New York plover population increased up to 35% (from 257 pairs to 332 pairs), following Hurricane Sandy and had relatively high reproductive output from 2014–2017 (USFWS 2018). This corresponding increase is suggestive of some degree of population synchrony, possibly due to other sites having been affected by Hurricane Sandy, and this regional increase may have been the source for the immigrants in our study area. However, other surrounding states, such as New Jersey, did not have a population increase but did have reasonably high reproductive output, some of which were confirmed to have immigrated into our population (USFWS 2018; M. Stantial, personal communication). Understanding the effect of the disturbance event of Hurricane Sandy on the regional population and analyzing these data at broader scales may provide additional information about population-level effects and whether immigration and emigration are significant at broader scales.

Some models that estimate population change assume that immigration is equal to emigration, which we have shown to be inaccurate for this increasing population (Schaub et al. 2013; Figure 4). However, equality of the two vital rates may be more likely if the population is stationary or the study site encompasses a larger area. With expanding plover population monitoring, we are increasingly able to detect the movement of individuals. We have confirmed immigration into our population from birds banded in New Jersey (~150km) and emigration from our population to Connecticut, Delaware, Rhode Island, New Jersey, and North Carolina, suggesting that the Fire Island population may be acting as a source (Pulliam 1988). However, we found correlation between immigration and population change, suggesting for this population

to continue to increase, the surrounding populations also need to be producing dispersing young or adults. Furthermore, for immigration and reproductive output to continue to have positive effects on population growth, there needs to be available habitat for the incoming birds to nest. The relationship between population change and immigration highlights how the Atlantic Coast plover population is acting as a metapopulation, and to better understand what is occurring at a single site, we need to understand regional patterns.

Future use of this model, or the models within, can help managers understand the effect of habitat, weather, or other factors on the components of population change. We need more data to understand the relationship between these factors and population growth, but this model will easily allow incorporation of extra years of data or inclusion of additional sites. Without a time-series capturing a decline in population size following the post-hurricane and predator dynamics, it would be particularly challenging to use these data to forecast into the future. This model, which explicitly incorporates the components of reproductive output, elements that are regularly collected with high degrees of precision, also can be used as a tool for managing many bird populations, particularly ones that are heavily monitored like piping plovers (e.g., western snowy plovers, hooded plovers [*Thinornis rubricollis*]). Nest and chick survival are routinely estimated for plovers, and our young-survival parameterization of the Dail-Madsen model could easily be replaced with a Cormack Jolly Seber model for studies with regular resighting of individual chicks (Hunt et al. 2013, 2018b; Weithman et al. 2019).

Conclusion

Monitoring populations following widespread disturbance-driven landscape changes can assist in the understanding of population change and directing future management. We found that restoration areas were behaving similarly to the rest of the plover habitat on the island, increasing

in pairs as the rest of the population increased. Therefore, restoration areas may be an effective way to promote plover populations on the Atlantic Coast, particularly if predictions of use are updated as new information becomes available. As is to be expected with early-successional habitats, both restoration areas have had increasing vegetation cover since their creation, although revegetation rates have differed, likely due to differences in construction techniques (Bellman 2018). As vegetation continues to grow and the time since Hurricane Sandy increases, vegetation removal will be required across our study site to maintain open, sparsely vegetated sand. That we found immigration to have the greatest correlation with population growth highlights the importance of regional management and cooperation among managing agencies to improve the population persistence of Fire Island and the entire Long Island area. Efforts to improve overall reproductive output are likely to only affect population growth if there is suitable habitat to support new individuals. Regional management to improve reproductive output, producing individuals to immigrate, also will help to sustain this population. We expect that the population will continue to increase, provided habitat remains for new immigrants and natal recruits.

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Tables

Table 1. Year-specific population size and composition estimated from an integrated population model fit to piping plover data from Fire and Westhampton Islands, 2013–2018. Values presented are the mean $\pm$ standard deviation.

Year	N _{tot}	N _{SY}	N _{ASY}	N _{Imm}	N _{ASY,emigrants}	N _{SY,emigrants}
2013	64	-	-	-	-	-
2014	65 $\pm$ 12	3 $\pm$ 2	34 $\pm$ 4	29 $\pm$ 13	12 $\pm$ 3	4 $\pm$ 2
2015	70 $\pm$ 13	11 $\pm$ 4	34 $\pm$ 7	26 $\pm$ 14	12 $\pm$ 4	17 $\pm$ 6
2016	76 $\pm$ 12	5 $\pm$ 3	37 $\pm$ 8	35 $\pm$ 14	13 $\pm$ 4	7 $\pm$ 3
2017	92 $\pm$ 13	19 $\pm$ 5	40 $\pm$ 8	35 $\pm$ 15	14 $\pm$ 5	29 $\pm$ 7
2018	114 $\pm$ 14	16 $\pm$ 5	49 $\pm$ 9	49 $\pm$ 16	17 $\pm$ 5	25 $\pm$ 6

Table 2. Year-specific proportional population composition estimated from an integrated population model fit to piping plover data from Fire and Westhampton Islands, 2013–2018.

Values presented are the mean $\pm$ standard deviation.

Year	Proportion SY	Proportion ASY	Proportion Immigrants
2013	-	-	-
2014	0.044 $\pm$ 0.034	0.54 $\pm$ 0.12	0.42 $\pm$ 0.13
2015	0.16 $\pm$ 0.069	0.50 $\pm$ 0.11	0.34 $\pm$ 0.14
2016	0.063 $\pm$ 0.036	0.50 $\pm$ 0.12	0.44 $\pm$ 0.13
2017	0.20 $\pm$ 0.064	0.43 $\pm$ 0.093	0.36 $\pm$ 0.12
2018	0.15 $\pm$ 0.048	0.44 $\pm$ 0.087	0.42 $\pm$ 0.10

Table 3. Year-specific demographic rates estimated from an integrated population model fit to Piping Plover data from Fire and Westhampton Islands, 2013–2018. Values presented are the mean $\pm$ standard deviation.

Year	Nest success	Chick survival	Reproductive output	Lambda	Immigration rate	Natal recruitment rate
2013	0.46 $\pm$ 0.12	0.19 $\pm$ 0.06	0.33 $\pm$ 0.14	-	-	-
2014	0.54 $\pm$ 0.11	0.62 $\pm$ 0.08	1.30 $\pm$ 0.30	1.01 $\pm$ 0.18	0.44 $\pm$ 0.19	0.049 $\pm$ 0.038
2015	0.34 $\pm$ 0.07	0.40 $\pm$ 0.07	0.52 $\pm$ 0.14	1.10 $\pm$ 0.26	0.40 $\pm$ 0.26	0.18 $\pm$ 0.085
2016	0.80 $\pm$ 0.07	0.61 $\pm$ 0.05	1.87 $\pm$ 0.22	1.11 $\pm$ 0.23	0.51 $\pm$ 0.23	0.073 $\pm$ 0.043
2017	0.62 $\pm$ 0.06	0.57 $\pm$ 0.05	1.34 $\pm$ 0.18	1.25 $\pm$ 0.25	0.47 $\pm$ 0.23	0.26 $\pm$ 0.088
2018	0.71 $\pm$ 0.06	0.72 $\pm$ 0.04	1.97 $\pm$ 0.19	1.25 $\pm$ 0.20	0.54 $\pm$ 0.20	0.19 $\pm$ 0.065

Table 4. Number of individuals per age class, in the population and that were estimated to have left the population. Estimates are from an integrated population model using piping plover data from Fire and Westhampton Islands, 2013–2018. The restoration areas were built between the 2014 and 2015 breeding seasons, and were created to mimic natural plover habitat, mitigating for potential plover habitat degradation following island stabilization efforts. Values reported are mean $\pm$ standard deviation.

Year	N _{tot}	N _{SY}	N _{ASY}	N _{Imm}	N _{ASY,emigrants}	N _{SY,emigrants}
Study area minus restoration area						
2014	63 $\pm$ 6	5 $\pm$ 3	32 $\pm$ 4	27 $\pm$ 9	13 $\pm$ 1	4 $\pm$ 2
2015	56 $\pm$ 7	17 $\pm$ 5	31 $\pm$ 5	10 $\pm$ 8	13 $\pm$ 2	16 $\pm$ 4
2016	64 $\pm$ 4	8 $\pm$ 4	28 $\pm$ 5	32 $\pm$ 9	12 $\pm$ 2	7 $\pm$ 3
2017	78 $\pm$ 4	23 $\pm$ 6	34 $\pm$ 5	23 $\pm$ 9	14 $\pm$ 1	21 $\pm$ 4
2018	100 $\pm$ 5	22 $\pm$ 6	39 $\pm$ 5	39 $\pm$ 10	16 $\pm$ 2	19 $\pm$ 4
Restoration areas						
2016	8 $\pm$ 4	1 $\pm$ 1	3 $\pm$ 2	4 $\pm$ 4	5 $\pm$ 1	2 $\pm$ 1
2017	12 $\pm$ 4	1 $\pm$ 1	2 $\pm$ 2	9 $\pm$ 4	3 $\pm$ 2	3 $\pm$ 1
2018	17 $\pm$ 4	2 $\pm$ 2	4 $\pm$ 2	11 $\pm$ 5	5 $\pm$ 2	5 $\pm$ 2

Figures

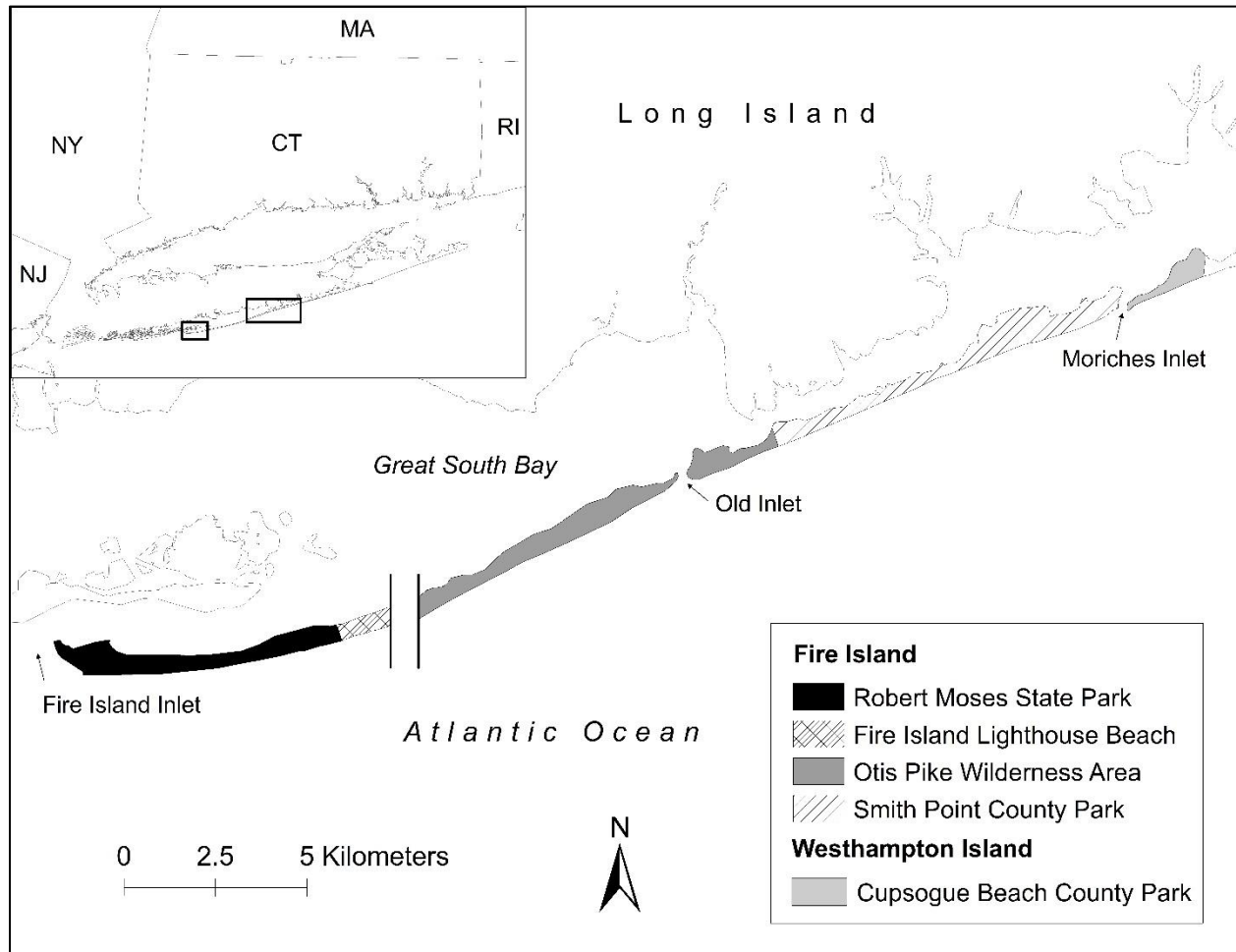


Figure 1. Study area on Fire and Westhampton Islands, NY in which piping plovers were studied 2013–2018. The break represented a ~25km area that we did not regularly survey for piping plovers. Nesting piping plover density was low to zero in this area from 2013–2018. Two restoration areas were created between the 2014 and 2015 breeding season were located at Smith Point County Park, one at the far eastern part of the study area and one in the middle (see Figure 2).



Figure 2. Two restoration areas created to mitigate for potential effects of barrier island stabilization to piping plovers on Fire Island, New York. Great Gun restoration area was 34.8ha and New Made Restoration area was 6.6ha (areas calculated 2015). Outlines are overlaid on imagery flown on March 3, 2016. Scale for the two images is the same for direct comparison. The two restoration areas are approximately 2.5km apart.

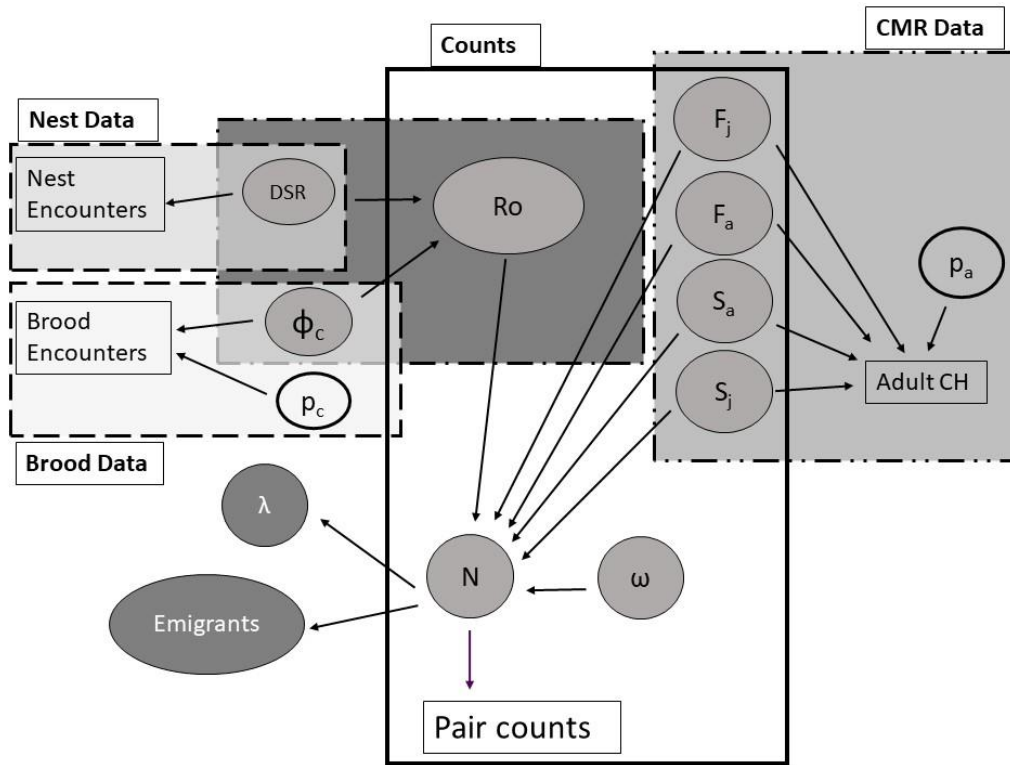


Figure 3. Integrated population model. The filled circles indicate parameters, with the light grey indicating estimated parameters and the dark grey indicating derived parameters. Open boxes indicate data. Open bolded circles indicate detection parameters. Adult CH indicates adult capture histories, CMR indicates capture-mark-recapture data, ω indicates number of immigrants, F indicates fidelity, S indicates true survival, p indicates detection probability, ϕ indicates survival, DSR indicates daily nest survival rate, R_o indicates reproductive output and N indicates population size.

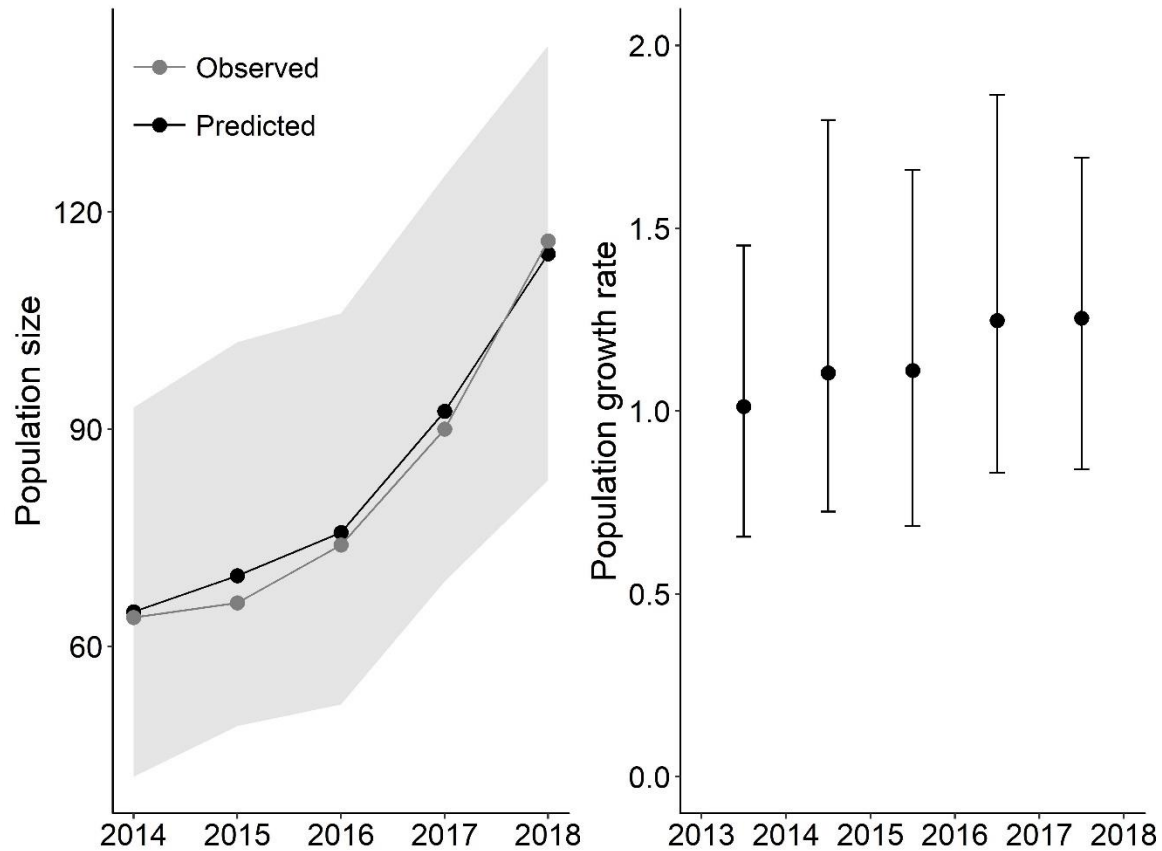


Figure 4. Estimated population size for a population of Piping Plovers on Fire and Westhampton Islands, New York. Estimates are from a state-space model within an integrated population model. The grey shaded area represents the 95% credible intervals on the predicted population size for each year. The population size for 2013 was set to 64 individuals, without error, and is not shown here.

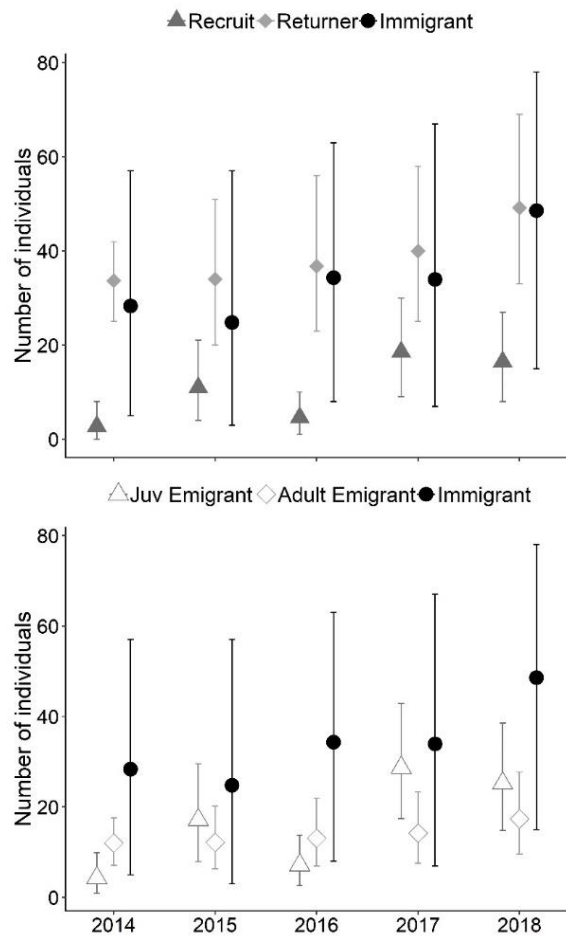


Figure 5. The number of each class of piping plovers predicted to be in the population each year (top) following the first year of a study on Fire and Westhampton Islands, estimated using an integrated population model, and the number of birds predicted to have left the population each year following the first year of the study with the number of immigrants for comparison (bottom). Recruits hatched in the study and returned to nest the following year, returners bred in the study area prior, and immigrants were new to the breeding population. Juvenile emigrants hatched in the study area and survived but did not breed in our study area the following year, and adult emigrants bred in our study in the year prior and survived but did not breed in our study area the following year.

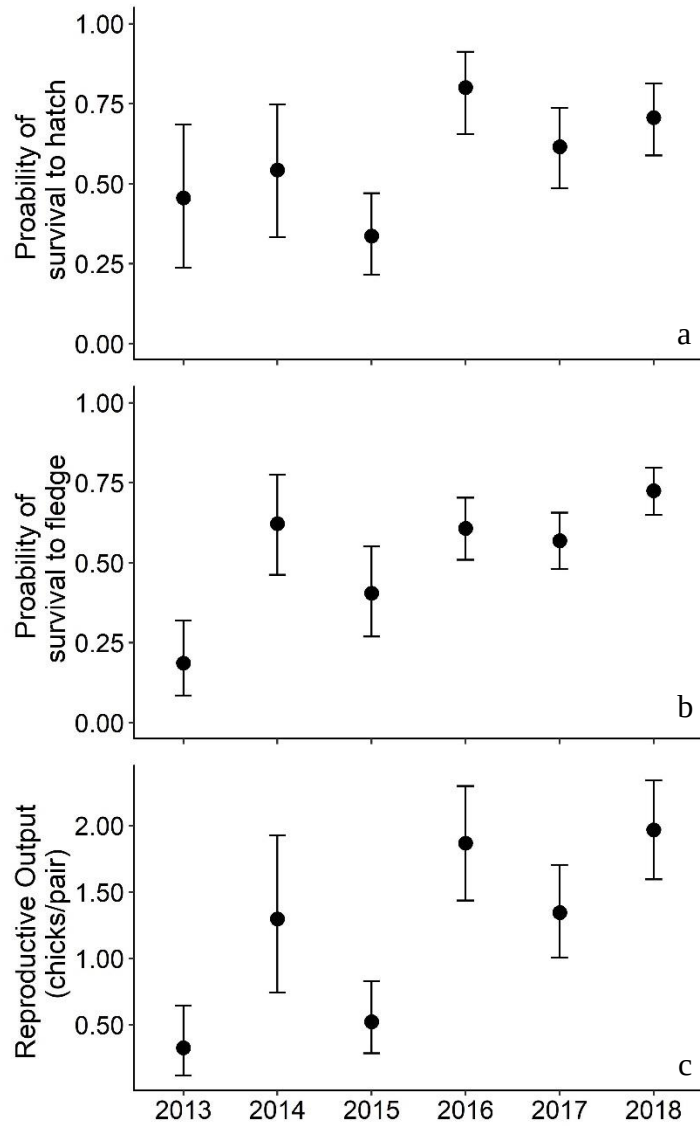


Figure 6. Reproductive output results from a piping plover integrated population model fit with data from Fire and Westhampton Islands, 2013–2018. Nest survival (a) was estimated using a logistic exposure model, Chick survival (b) was estimated using a Dail-Madsen model and Reproductive output (c) was estimated by taking the product of nest survival, chick survival, and average clutch size ($\bar{x} = 3.84$ eggs) and dividing by the number of pairs in the population.

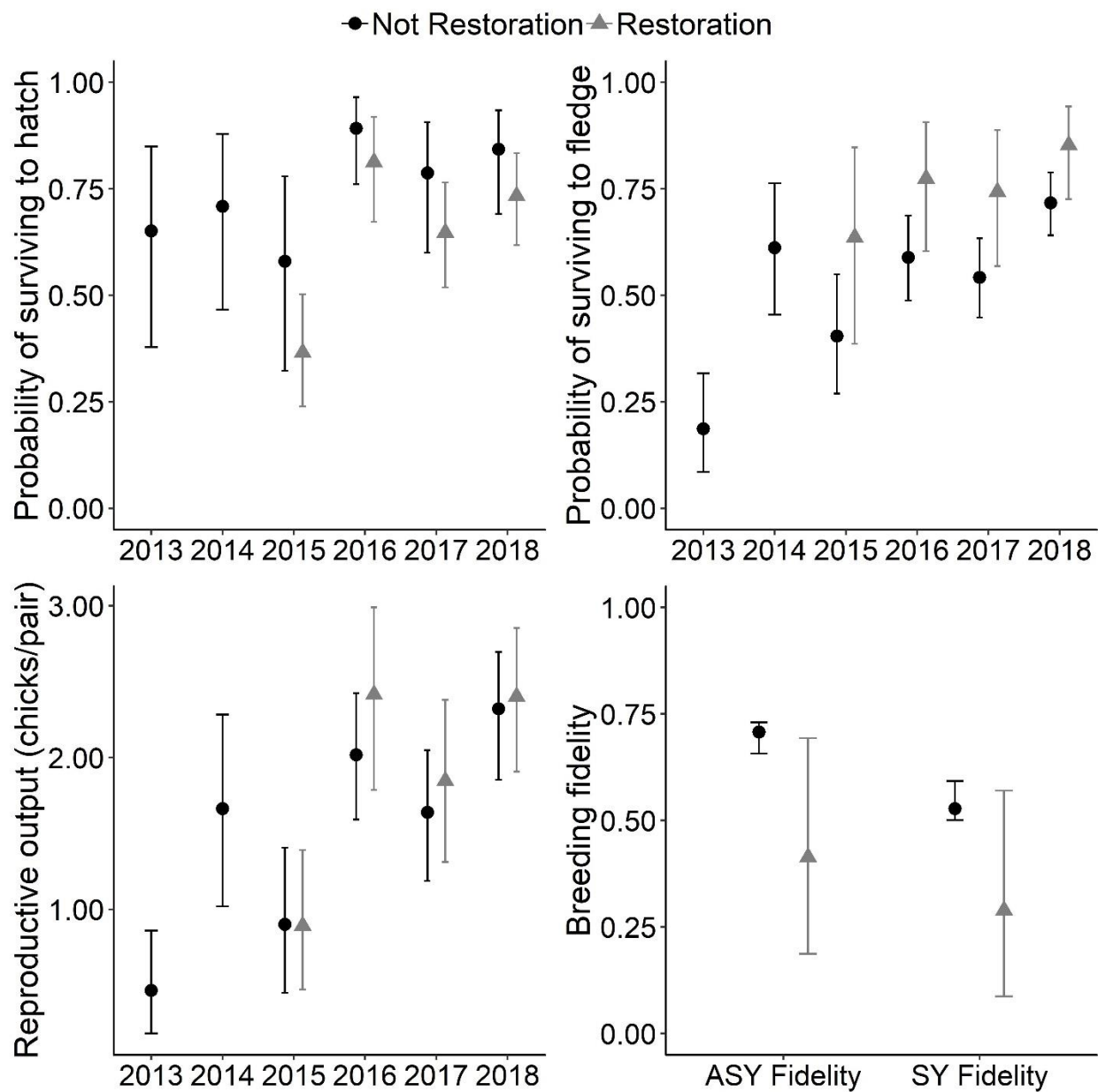


Figure 7. Demographic estimates from an integrated population model estimating the effect of restoration areas on piping plover population change on Fire and Westhampton Islands, 2013–2018. The restoration areas were built between the 2014 and 2015 breeding season, so estimates are only shown for the restoration areas 2015–2018.

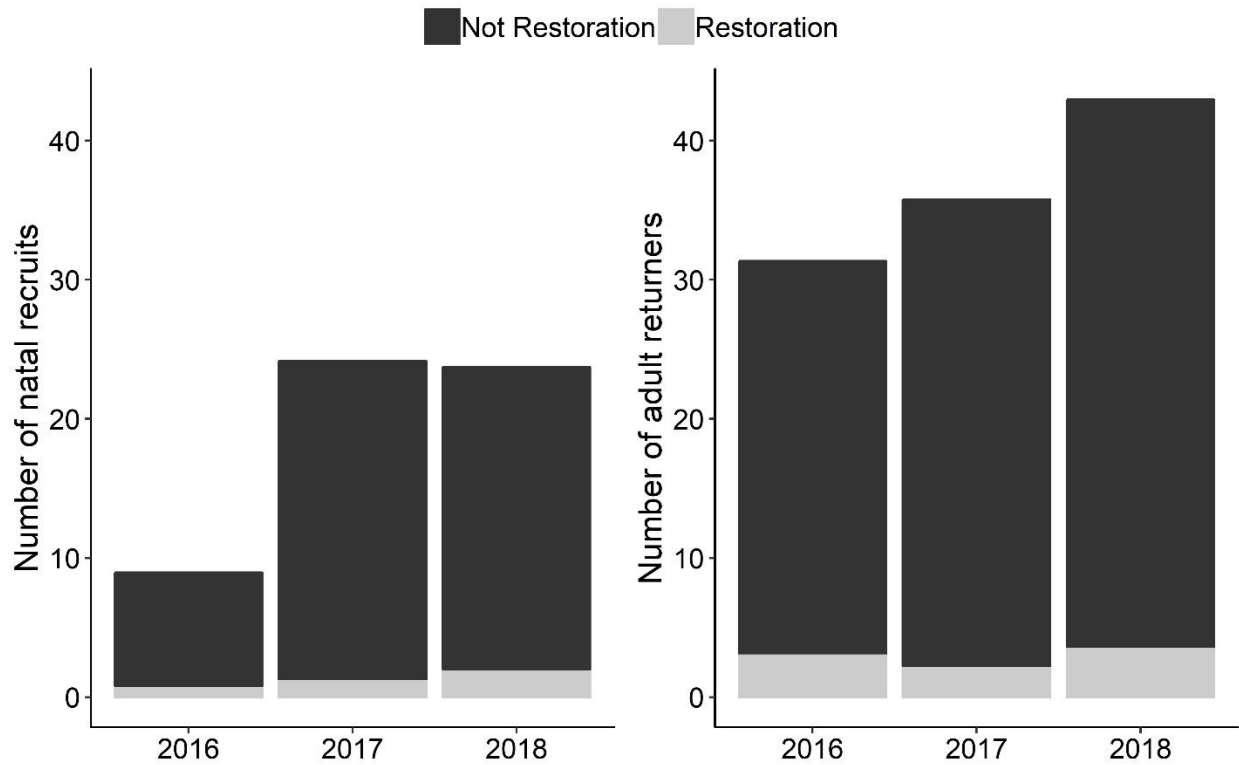


Figure 8. The number of natal recruits and adult returning plovers contributed from USACE-built restoration areas in the year prior. Estimates are from an Integrated Population Model, and estimates are derived from the number of fledglings multiplied by the survival and fidelity rate of fledglings for SY and the number of adults in the restoration areas multiplied by the survival and fidelity rate of adults for ASY. Restoration areas were built in 2015.

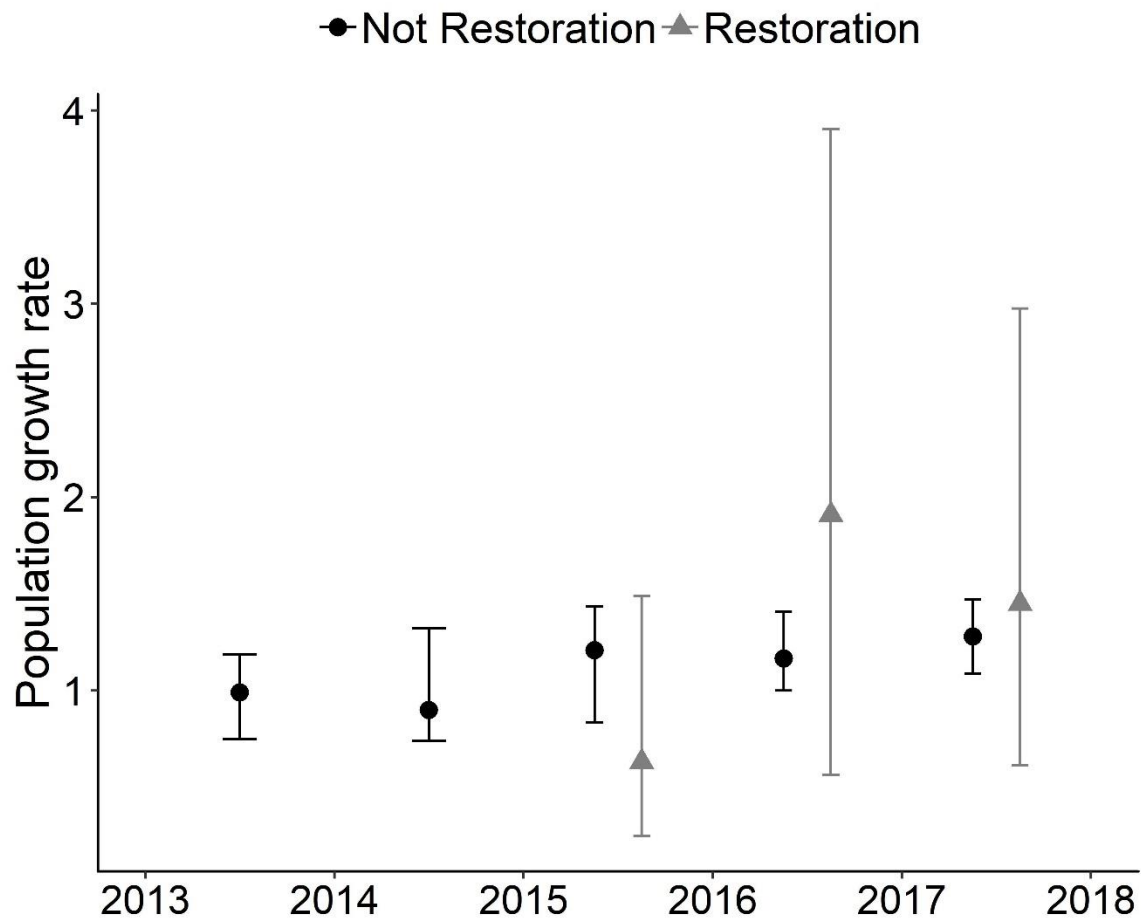


Figure 9. Comparison of population growth rate for plover restoration areas 2013–2018 derived from an integrated population model. Restoration area estimates are only shown following the 2015 breeding season as the restoration areas were built between the 2014 and 2015 breeding seasons.

Appendix B. Data and apparent estimates from 2013–2018 piping plover monitoring on Fire Island and Westhampton Island

Table 5. Raw field data and apparent demographic estimates for Fire Island and Westhampton Island piping plover monitoring, 2013–2018. In 2013 and 2014, we did not monitor Robert Moses State Park or the Fire Island Lighthouse Beach (Figure 1).

	Raw			Raw		Raw	
	# Nests	#	nest	# Chicks	#	chick	reproductive
Year	monitored	Hatched	success	monitored	Fledged	success	output
2013	20	11	0.55	40	9	0.23	0.47
2014	20	11	0.55	43	24	0.56	1.14
2015	48	16	0.33	46	13	0.28	0.39
2016	40	33	0.83	109	63	0.58	1.75
2017	61	40	0.66	135	70	0.52	1.44
2018	68	50	0.74	183	117	0.64	1.98

Appendix C. Supplementary model code for integrated population model

Supplementary material.

Model code for Integrated Population Model implemented in JAGS.

Integrated population model (IPM) for Fire Island NY piping plovers, 2013-2018

Sarah Saunders, Francesca Cuthbert, Elise Zipkin

Required packages

library(jagsUI) #load the jagsUI library

#####

Adapted from original scripts by Marc Kéry & Michael Schaub (2016), adapted by S. Saunders, 2016 – 2017 (Saunders et al. 2018)

#Models

#State space model for estimating population size

#Barker model for estimating true adult survival

#Modified Dail-Madsen model for estimating chick survival

#Logistic exposure model for estimating nest survival

#Data definitions

nyears #number of years of the study

pairs #Number of individuals in each year

#Barker Model#

barker.ch #barker capture history, individual x year

n.ind #number of individuals

#Function to create matrix of first capture

get.first <- function(x){min(which(x != 0))}

first <- apply(barker.ch, 1, get.first)

z.init.barker <- matrix(2, nrow(barker.ch), ncol(barker.ch))

for (i in 1:nrow(barker.ch)){

 z.init.barker[i,(1:first[i])] <- NA

}

#Chick Survival Model#

y #brood capture history

n.broods #number of broods

n.occasions= #number of occasions in brood capture history (5 here)

occasion.v #vector of occasions

year.id.c #brood specific vector of year

#Nest Survival Model#

year.id.n #vector of nest visit year

interval #vector of interval between nest visits

succ #vector of nest successes and failures

```
#Max Clutch Model
```

```
maxegg #vector of clutch size for each nest that reached full clutch
```

```
sink("pipl.ipm.bark.jags")
```

```
cat(" "
```

```
  model {
```

```
    #-----
```

```
    # Integrated population model
```

```
    # - Age structured model with 2 age classes:
```

```
    #       SY and ASY
```

```
    # - Age at first breeding = 1 year
```

```
    # - Immigration and Reproductive Output assumed to be time dependent
```

```
    # - Explicit estimation of immigration
```

```
    #-----
```

```
    #-----
```

```
    # 1. Define the priors for the parameters
```

```
    #-----
```

```
    # Initial population sizes
```

```
    Ntot[1] <- pairs[1] #Set the initial population size
```

```
    # Mean demographic parameters (on appropriate scale)
```

```
    mean.phij ~ dunif(0,1) #prior for SY survival
```

```
    mean.phia ~ dunif(0,1) #prior for ASY survival
```

```
    mean.Fa ~ dunif(0,1) #prior for ASY fidelity
```

```
    mean.Fj ~ dunif(0,1) #prior for SY fidelity
```

```
    mean.Imm ~ dunif(0, 100) #expected number of immigrants on real scale
```

```
    p ~ dbeta(1,1) #capture probability
```

```
    f <- 0 #band recovery probability
```

```
    R ~ dbeta(1,1) #non-breeding resight probability given survival from t to t+1
```

```
    Rp ~ dbeta(1,1) #non-breeding resight probability given mortality during interval t to t+1
```

```
    for(t in 1:(nyears-1)){
```

```
      beta.imm[t] ~ dnorm(0,0.001) #prior for fixed effect of annual variation in immigration
```

```
    }
```

```
    beta.imm[nyears] <- 0
```

```
    #State Space Model Precision of standard deviations of temporal variability
```

```
    sig.obs ~ dunif(0.5, 50)
```

```
    tau.obs <- pow(sig.obs, -2)
```

```

#-----
# 2. Constrain parameters
#-----
for (t in 1:(nyears-1)){
  logit(phia[t]) <- mu.phia # Adult true' survival
  logit(phij[t]) <- mu.phij # Juvenile 'true' post-fledge
  logit(Fa[t]) <- mu.Fa    # Juvenile fidelity
  logit(Fj[t]) <- mu.Fj    # Adult fidelity
  omega[t] <- mean.imm + beta.imm[t] # Immigration (fixed effect of year)
}

#-----
# 3. Derived parameters
#-----
mu.phia <- log(mean.phia / (1-mean.phia)) #ASY survival on logit scale
mu.phij <- log(mean.phij / (1-mean.phij)) #SY survival on logit scale
mu.Fa <- log(mean.Fa / (1-mean.Fa)) #ASY fidelity on logit scale
mu.Fj <- log(mean.Fj / (1-mean.Fj)) #SY fidelity on logit scale

# Population growth rate
for (t in 1:(nyears-1)){
  lambda[t] <- Ntot[t+1] / (Ntot[t])          #Population growth rate
  logla[t] <- log(lambda[t])
  imrate[t] <- Nadimm[t+1] / Ntot[t]          # Derived immigration rate
  newrate[t] <- (Nadimm[t+1] + N1[t+1]) / Ntot[t] #Derived total recruitment rate
  n.recruirate[t] <- (N1[t+1] / Ntot[t])       #Derived natal recruitment rate
}
for (t in 2:nyears){
  Emigranta[t] <- Ntot[t-1] * phia[t-1] * (1-Fa[t-1]) #Derived number of ASY emigrants
  Emigrantj[t] <- fledglings[t-1] * phij[t-1] * (1-Fj[t-1]) #Derived number of SY
emigrants
  EmigrantT[t] <- Emigranta[t] + Emigrantj[t] #Total number of emigrants
  a.emrate[t] <- Emigranta[t] / Ntot[t-1] #ASY Emigration Rate
  j.emrate[t] <- Emigrantj[t] / fledglings[t-1] #SY Emigration Rate
}

mlam <- exp((1/(nyears-1))*sum(logla[1:(nyears-1)])) # Geometric mean population
growth rate

#-----
# 4. The likelihoods of the single data sets
#-----
# 4.1. Likelihood for population count data (state-space model)
# 4.1.1 System process

```

```

for (t in 2:nyears){
  N1[t] ~ dbin(phiij[t-1]*Fj[t-1], fledglings[t-1]) #number of natal recruits in year t is a
function of post-fledge survival, and the number of fledglings from the year prior
  NadSurv[t] ~ dbin(phia[t-1]*Fa[t-1], Ntot[t-1]) #number of surviving adults in year t is a
function of adult survival and the total number of adults in year T
  Nadimm[t] ~ dpois(omega[t-1])
}

```

```

# 4.1.2 Observation process
for (t in 2:nyears){
  Ntot[t] <- NadSurv[t] + N1[t] + Nadimm[t] #Total individuals in year t
  pairs[t] ~ dnorm(Ntot[t], tau.obs)
  Prop_N1[t] <- N1[t] / (Ntot[t]+0.1) #Proportion natal recruits make up total
  Prop_NadSurv[t] <- NadSurv[t] / (Ntot[t]+0.1) #Proportion adult returners make up
total
  Prop_NadImm[t] <- Nadimm[t] / (Ntot[t]+0.1) #Proportion immigrants make up total
}

```

```

#####
#####

```

```

#-----
# Parameters:
# phi: survival probability
# F: site fidelity
# p: capture probability
# R: non-breeding resight probability given survival from t to t+1
# Rp (R'): non-breeding resight probability given mortality during interval t to t+1
# f: band recovery probability
#-----

```

```

#####
#####

```

```

#####
#####

```

```

#-----
# Latent states (Psi):
# 1) alive as juvenile
# 2) alive, available
# 3) alive, unavailable
# 4) alive, permanent emigrant
# 5) recently dead, resighted
# 6) dead in previous interval

```

#-----

#####

#####

Juvenile transitions

for(t in 1:(nyears-1)){

Psi[1,t,1] <- 0

Can't stay young after first year

Psi[1,t,2] <- phij[t] * Fj[t]

Survive as juvenile and return as adult

Psi[1,t,3] <- phij[t] * (1-Fj[t])

Survive as juvenile and emigrate

Psi[1,t,4] <- 0

Psi[1,t,5] <- 0

Psi[1,t,6] <- (1 - phij[t])

Die as juvenile

Adult transitions

Psi[2,t,1] <- 0

Entry is conditional on first capture

Psi[2,t,2] <- phia[t] * Fa[t]

Alive as adult, faithful

Psi[2,t,3] <- phia[t] * (1-Fa[t])

Alive as adult, notfaithful

Psi[2,t,4] <- f

Died, recovered

Psi[2,t,5] <- (1 - phia[t]) * Rp

Seen elsewhere, but died prior to returning

Psi[2,t,6] <- (1 - phia[t]) * (1 - Rp) - f

Died, and never seen

Unfaithful transitions

Psi[3,t,1] <- 0

Psi[3,t,2] <- 0

Psi[3,t,3] <- phia[t]

Survive as a emigrant

Psi[3,t,4] <- f

Died as an emigrant

Psi[3,t,5] <- (1 - phia[t]) * Rp

Psi[3,t,6] <- (1 - phia[t]) * (1 - Rp) - f

Shot transitions

Psi[4,t,1] <- 0

Psi[4,t,2] <- 0

Psi[4,t,3] <- 0

Psi[4,t,4] <- 0

Psi[4,t,5] <- 0

Psi[4,t,6] <- 1

Natural mortality transitions (seen before death)

Psi[5,t,1] <- 0

Psi[5,t,2] <- 0

Psi[5,t,3] <- 0

Psi[5,t,4] <- 0

Psi[5,t,5] <- 0

Psi[5,t,6] <- 1

Natutal mortality transitions (not seen before death)

Psi[6,t,1] <- 0

Psi[6,t,2] <- 0

Psi[6,t,3] <- 0

Psi[6,t,4] <- 0

Psi[6,t,5] <- 0

```
Psi[6,t,6] <- 1
}
```

```
#####
#####
```

```
#-----
```

```
# Breeding observations (o ~ Omega):
```

```
# 1) seen as juvenile (not possible): Confusing, but the true state is assigned on the
first occasion, so all juvenile observations are assigned, none are estimated.
```

```
# 2) seen breeding adult, seen non-breeding
```

```
# 3) seen breeding adult, not seen non-breeding
```

```
# 4) not seen breeding, seen non-breeding
```

```
# 5) not seen breeding, not seen non-breeding
```

```
# 6) shot
```

```
#-----
```

```
#####
#####
```

```
Omega[1,1] <- 0
```

```
Omega[1,2] <- 0
```

```
Omega[1,3] <- 0
```

```
Omega[1,4] <- 0
```

```
Omega[1,5] <- 1
```

```
Omega[1,6] <- 0
```

```
Omega[2,1] <- 0
```

```
Omega[2,2] <- p*R
```

```
Omega[2,3] <- p*(1 - R)
```

```
Omega[2,4] <- (1 - p)*R
```

```
Omega[2,5] <- (1 - p)*(1 - R)
```

```
Omega[2,6] <- 0
```

```
Omega[3,1] <- 0
```

```
Omega[3,2] <- 0
```

```
Omega[3,3] <- 0
```

```
Omega[3,4] <- R
```

```
Omega[3,5] <- (1 - R)
```

```
Omega[3,6] <- 0
```

```
Omega[4,1] <- 0
```

```
Omega[4,2] <- 0
```

```
Omega[4,3] <- 0
```

```
Omega[4,4] <- 0
```

```
Omega[4,5] <- 0
```

```
Omega[4,6] <- 1
```

```
Omega[5,1] <- 0
```

```
Omega[5,2] <- 0
```

```
Omega[5,3] <- 0
```

```
Omega[5,4] <- 1
```

```
Omega[5,5] <- 0
```

```
Omega[5,6] <- 0
```

```
Omega[6,1] <- 0
```

```
Omega[6,2] <- 0
```

```
Omega[6,3] <- 0
```

```
Omega[6,4] <- 0
```

```
Omega[6,5] <- 1
```

```
Omega[6,6] <- 0
```

```
# Likelihood
```

```
for (i in 1:n.ind){
```

```
  z[i, first[i]] <- ch[i,first[i]]
```

```
  for (t in (first[i] + 1):nyears){
```

```
    z[i,t] ~ dcat(Psi[z[i,t-1],t-1, ])
```

```
    ch[i,t] ~ dcat(Omega[z[i,t], ])
```

```
  }
```

```
}
```

```
#####  
####
```

```
# Dail-Madsen Model Priors (Chick Survival - Count Based)
```

```
#####  
####
```

```
#####
```

```
# Model suffers from confounding between final p and phi
```

```
#####
```

```
mean.phic ~ dunif(0,1) #Prior for mean chick survival
```

```
mu.phic <- log(mean.phic/(1-mean.phic)) #Logit transformation
```

```

    mixing ~ dbeta(2.5, 25) #Constant brood immigration parameter, brood emigration is
    constrained with phi

```

```

    for(t in 1:(nyears-1)){
    beta.year.c[t] ~dnorm(0,0.001) #Fixed effect of year
    }
    beta.year.c[nyears] <- 0
    beta.time.c ~ dnorm(0,0.001)

```

```

    for (v in 1:(n.occasions - 2)){
    count.p[v] ~ dunif(0, 1) #Probability of detection
    }
    count.p[(n.occasions - 1)] <- count.p[(n.occasions-2)]

```

```

    for(t in 1:nyears){
    for (v in 1:(n.occasions - 1)){
    logit(year.phi[t,v]) <- mu.phic + beta.year.c[t] + beta.time.c*occasion.v[v] #Predicts
    annual chick survival with separate fixed effects of time and occasion
    }
    }

```

```

    for(w in 1:n.broods) {
    for (v in 1:(n.occasions - 1)){
    logit(phi[w,v]) <- mu.phic + beta.year.c[year.id.c[w]] + beta.time.c*occasion.v[v]
    }
    }

```

```

#####
# Model
#####
# Assign constraints on initial brood size
for(w in 1:n.broods) {

```

```

    N[w,1] <- y[w,1] # Model assumes perfect detection of initial brood sizes

```

```

#####
#
# S: Number of individuals that survived (latent state)
# G: Number of individuals that immigrated into brood (latent state)
# N: Number of individuals associated with a brood (latent state)
# y: encounter history

```

```
#####
#
  for(v in 2:n.occasions) {
    S[w,v-1] ~ dbin(phi[w,v - 1] * (1 - mixing), N[w,v-1])
    G[w,v-1] ~ dpois(mixing * N[w,v-1] * phi[w, v - 1])
    N[w,v] <- S[w,v-1] + G[w,v-1]
    y[w,v] ~ dbin(count.p[v - 1], N[w,v])
  }

  for (t in 1:nyears){
    for(v in 1:n.occasions) {
      Nt[t,w,v] <- ifelse(year.id[w] == t, N[w,v], 0)
    }
  }
  for (t in 1:nyears){
    annual.phi[t] <- prod(year.phi[t,]) #Derived annual chick survival
    for(v in 1:n.occasions){
      Nyear[t,v] <- sum(Nt[t,1:n.broods,v]) #Estimated number of chicks alive at each
occasion
    }
  }

#####
####Logistic Exposure#####
#####Nest Survival#####
#####

#Prior distributions on parameters
a.0 ~ dnorm(0, .001) ##Center prior for intercept at a reasonable value on probability
scale for a daily survival probability

for(t in 1:(nyears-1)){
  beta.year.n[t] ~ dnorm(0,0.001) #Fixed effect of year
}
beta.year.n[nyears] <- 0

for(d in 1:length(succ)){
  eta[d] <- a.0 + beta.year.n[year.id.n[d]]

  expeta[d] <- exp(eta[d])
  s[d] <- expeta[d] / (1+ expeta[d])
  season[d] <- pow(s[d], interval[d])
  succ[d] ~ dbern(season[d])
} #d

```

```
#####
#####Egg Mass#####
#####
mu.egg ~ dnorm(0,.001)
tau.egg <- pow(sigma.egg, -2)
sigma.egg ~ dunif(0,100)

for (q in 1:length(maxegg)){
  maxegg[q] ~ dnorm(mu.egg, tau.egg)
}

#####Derived Parameters#####
# expected mean number of total fledglings based on demographic parameters
for (t in 1:nyears){
  annual.ns[t] <- pow((exp(a.0+beta.year.n[t])/(1+exp(a.0+beta.year.n[t]))), 33)

  Ro[t] <- mu.egg*annual.phi[t]*annual.ns[t] #Reproductive output (fledglings/pair)

  fledglings[t] ~ dpois(Fledge[t])
  Fledge[t] <- pairs[t]*Ro[t]*0.5 #Number of fledglings. 0.5 because pairs is number of
  individuals

}##t

}
",fill = TRUE)
sink()

# Bundle data
Ni <- y + 10
Si <- Ni[,2:n.occasions]
Si[] <- 1
Gi <- Ni[,-1]-Si
Ni[,-1] <- NA

jags.data <- list(nyears = nyears, ch = barker.ch, n.ind = dim(barker.ch)[1], first=first,
pairs = pairs,
  n.broods=dim(y)[1], n.occasions= dim(y)[2], y=y,
  year.id.n=data$year.n, interval=data$interval, succ=data$succ,
  maxegg=eggcount, occasion.v = occasion.v, year.id.c = year.id.c
)

# Initial values
inits <- function(){list(S=Si, G=Gi, z = z.init.barker)}
```

```

# Parameters monitored
parameters <- c('lambda', 'phia', 'phij', 'Fa', 'Fj', 'p', 'R', 'Rp', 'f', 'mlam', "sig.obs", "N1",
"NadSurv", "Ntot", "omega", "Nadimm", "imrate",
    "mixing", 'annual.phi', "a.0", "beta.year.n", "annual.ns", "Ro",
"mean.egg", "sigma.egg", "alpha.egg", "fledglings", "Fledge",
    "Emigranta", "Emigrantj", "newrate", "mean.phij", "mean.phia", "mu.phia",
"mu.phij", "mu.phi", "mu.Fa", "mu.Fj",
    "beta.year.c", "beta.time.c", "beta.imm", "EmigrantT", "Prop_N1",
"Prop_NadSurv", "Prop_NadImm", "n.recruirate", "count.p", "a.emrate", 'j.emrate')

#MCMC settings
ni <- 100000
nt <- 2
nb <- 30000
nc <- 3
na <- 30000

# Call JAGS from R
pipl.ipm.barker <- jags(jags.data, inits, parameters, "pipl.ipm.bark.jags", n.chains = nc,
n.adapt = na, n.thin = nt, n.iter = ni, n.burnin = nb, parallel = TRUE, store.data = TRUE)

```

CHAPTER 3. PIPING PLOVER HABITAT SELECTION VARIES BY BEHAVIOR

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Piping plover habitat selection varies by behavior

Samantha Robinson^{1†}, Henrietta Bellman^{1,2}, Katie Walker¹, Daniel Catlin¹, Sarah Karpanty¹,
Shannon Ritter¹, and James Fraser¹

¹Virginia Tech, 310 W. Campus Dr., Blacksburg, VA 24061, USA

²Delaware Division of Fish & Wildlife, 6180 Hay Point Lansing Rd, Smyrna, DE, USA 19977

† E-mail: samgr@vt.edu

Abstract

Piping plover (*Charadrius melodus*, ‘plover’) are beach-nesting shorebirds that breed from April through September. When plovers arrive on the breeding grounds, they select and defend territories, lay and incubate eggs, tend to precocial broods, and return to a non-breeding stage after nest failure or chicks have fledged or died. Biological requirements and constraints may differ among these periods, therefore we hypothesized that habitat selection might also differ. We monitored plovers on Fire Island and Westhampton Island, New York during 2016–2018, and recorded individual locations of birds. We used model selection techniques to determine whether breeding stage (pre-breeding, nesting, brooding, post-breeding), simple breeding stage (breeding, not-breeding), or instantaneous behavior class (parental [incubating, brooding, and accompanying chicks], non-parental) best explained habitat selection during the 5-month plover breeding season. Model selection suggested that behavior class best explained habitat selection. Compared to non-parental plovers, plovers engaged in parental behavior selected areas closer to bay intertidal habitats and with more dry sand in the surrounding landscape. Non-parental plovers avoided areas with more dry sand and did not select for or against bay intertidal habitats. Additionally, non-parental plovers avoided development and higher elevation more than parental plovers, although both exhibited avoidance of these features. In each year, there was more suitable habitat for parental plovers than non-parental plovers, and the total amount of suitable habitat ranged from 100.14 ha to 151.07 ha. Due to these differences, when improving or creating plover habitat, managers should consider habitat needs both for parental and non-parental adult plovers, and protect habitat needed for both behavioral classes. Habitat management for nesting plovers should focus on maintaining vegetation-free sand and access to foraging habitat, as variables associated with these factors were influential for both behavior

classes, and habitat management for non-parental plovers should focus on low-elevation foraging habitats.

Key Words: *Charadrius melodus*; early-successional habitat; Hurricane Sandy; multi-scale modeling; suitable habitat; threatened species.

Introduction

Habitat conservation should be built on knowledge of animals' habitat selection, especially when managing imperiled species (Caughley 1994, Jones 2001). Resource managers can protect already suitable habitat, and less suitable habitat can be targeted for management. The choices that animals make on the landscape may be dictated by several co-occurring factors. For instance, habitat use or selection may differ between life stages, such as when individuals are actively rearing young versus preparing for migratory departure. Depending on the degree of difference, biological stage-specific habitat needs may have differing importance to the annual cycle (Ahlering and Faaborg 2006). However, behavior, rather than biological or breeding stage, may dictate habitat selection, and thus the two concepts should be compared and contrasted for a thorough understanding of birds reaction to landscape processes (Lima and Zollner 1996).

In dynamic systems, habitat conditions can rapidly change within and between years (Ray and Gregg, 1991), particularly in disturbance-dependent systems where a single event can cause widespread and long-lasting change (Walker and Schlacher 2011, Walker et al. 2019). Barrier islands, typically long sandy islands that lay adjacent to the mainland (Leatherman 1988), are dynamic within and between years. Within years, vegetation increases during the growing season, and between years, island geomorphology changes from storm and tidal energy. Species occupying dynamic landscapes may modify landscape interactions in response to temporal or spatial cues (Boulinier and Danchin 1997, Doligez et al. 2002).

Piping plovers (*Charadrius melodus*; plover), a federally threatened species, inhabit disturbance-dependent environments (Hunt et al. 2018b, Robinson et al. 2019). Plovers are migratory and likely interact with these landscapes in varying ways between breeding, migratory, and wintering sites (Fraser et al. 2005, Cohen et al. 2008a, Weithman et al. 2018). On the breeding grounds, plovers transition through a variety of breeding stages, such as territory establishment and courtship, initiating and incubating nests, tending to chicks, and preparing for southward migration (Elliot-Smith and Haig 2004). Because of different biological and spatial requirements within these stages, particularly needing foraging habitat that is accessible for flightless chicks during breeding (Walker et al. 2019, Zeigler et al. 2019, Maslo et al. 2019b), plovers may select habitat differently between stages. However, within breeding stages, adult plovers vary behaviorally between tending to their nests or chicks and foraging, and habitat selection may differ between these behavioral variations. Understanding whether differences among breeding stages or between behavioral states manifest in habitat selection can improve plover habitat management.

Plovers nest on Fire Island and Westhampton Island (hereafter; Fire Island), barrier islands off the south-shore of Long Island. Hurricane Sandy broadly affected Fire Island in the fall of 2012. Across Fire Island, much of the beach front was eroded (Hapke et al. 2013), but some beachfront and dune sand was transferred to overwash fans, wide swaths of sand that can extend across the entirety of an island (Walker et al. 2019). Dune loss could increase mainland vulnerability to future storm (Sallenger 2000) however, dune flattening also could benefit early-successional, disturbance-dependent species. Prior to Hurricane Sandy, plover habitat primarily was oceanfront sandy backshore habitats, backed by vegetated dunes (Walker et al. 2019). Widespread overwash creation facilitated comparison of plover habitat selection and suitability

across habitat types; pre-existing oceanfront sandy backshore habitat and newly created overwash fans.

Much of the existing habitat selection studies for plovers are nest-site selection studies, or were spatially implicit (Le Fer et al. 2008a, Maslo et al. 2016, Walker et al. 2019). Fine-scale selection studies have shown that nesting plovers select for areas with <20% vegetation cover, and areas of wide beach width (Maslo et al. 2011, Walker et al. 2019). Shell cover, distance to dune, amount of wrack, and distance to vegetation also have been significant predictors of plover nest locations (Burger 1987, Flemming et al. 1992, Boyne et al. 2014).

Despite assessments of nest-site selection, some adult plover habitat selection precedes that of nest-site selection, and adult plovers remain on the breeding grounds following nest hatch. Therefore, habitat selection analyses should consider the more varied adult plover habitat selection to ensure that suitable habitat is available throughout (Paterson et al. 2012). Habitat selection can differ between life stages due to differential food requirements or foraging abilities, movement ability, risk of predation, or thermoregulation abilities (Moermond 1979, Paasivaara and Pöysä 2008, Bloom et al. 2013). Unlike stationary nest locations, accurate locations of piping plovers are challenging to obtain due to efforts to reduce disturbance and a lack of fine-scale technology to mark a large sample of individuals. Spatially implicit studies on plover habitat selection show that plovers benefit from areas of low human use, allowing individuals to focus on foraging and resting rather than being alert (Burger 1994, DeRose-Wilson et al. 2018). Plover pair abundance was greater in the Great Plains when there was most nesting habitat (Anteau et al. 2014). Habitat selection for plover chicks suggests that moist and saturated habitat are more important than dry or densely vegetated habitats (Le Fer et al. 2008a).

Since biological requirements and constraints may differ among breeding stages, we hypothesized that habitat selection also might differ. Alternatively, habitat selection may reflect differences in behavior, as breeding adults may not be consistently tending to nests or chicks (Flemming 1987, Schneider and McWilliams 2007). Adult plover habitat selection also may vary among spatial scales because adults are highly mobile and likely perceive resource availability at multiple scales. Multi-scale habitat selection can refer to the specific size of the pixel, the size of the landscape, or the level of selection (i.e., second vs. third order selection; Johnson 1980, McGarigal et al. 2016). Here we use scale to reference the idea that habitat selection can occur at different spatial and temporal scales depending on the specific resource in question (Chambers et al. 2016, Timm et al. 2016). For example, plovers may evaluate foraging habitat at fine scales due to local invertebrate abundance variation, but may evaluate vegetation at broader scales to avoid predator encounters. Therefore, habitat selection studies should address questions of whether the scale of relationships varies via scale optimization (McGarigal et al. 2016), and whether relationships with the landscape change over time. These questions are especially crucial to address for plovers, which reside in highly dynamic habitats that can change annually (Bellman 2018). Furthermore, the plover population in our study area varied considerably between 2016 and 2018, increasing from 36 to 58 pairs (Walker et al. 2019). The population increase may have necessitated a change in habitat selection as nesting density increased.

Our objectives were to 1) determine if breeding stage or instantaneous behavior predicted adult plover habitat selection, 2) develop resource selection functions (RSF) for adult plovers, and 3) predict available habitat to 4) estimate if the amount of suitable habitat differs among stages/behaviors. We predicted that breeding stage, rather than behavior, would best predict habitat selection. We predicted that pre-breeding and nesting habitat selection of adults would be

similar. When birds arrive on the breeding grounds, they begin defending territories and creating potential nest sites (Cairns 1982). Therefore, based on past studies, we predicted that adults in these stages would select for areas of open, sparsely vegetated sand to increase camouflage and reduce detection of nests and chicks by terrestrial predators (Troschianko et al. 2016). We also predicted that brooding adults would select areas closer to intertidal foraging habitats, particularly low-energy intertidal habitats that are ideal for brood foraging (Elias et al. 2000), and that post-breeding adults would select areas closer to both high- and low-energy foraging habitats to increase fat reserves prior to departing for migration (Lindström and Piersma 1993). Finally, we predicted that suitable habitat would decrease between 2016 and 2018, as the vegetation cover in previously suitable habitat increased (Bellman 2018).

Material and Methods

Study area

We studied plovers on a 27-km stretch of Fire Island and Westhampton Island (Figure 1). We began recording of fine-scale adult locations in 2016, using positional geometry and location offset methods (Robinson et al. 2020). The study area consisted of Fire Island National Seashore, managed by the National Park Service, Smith Point, and Cupsogue Beach County Parks, managed by Suffolk County Parks, and Robert Moses State Park, managed by New York Parks, Recreation, and Historic Preservation. These islands have the Atlantic Ocean to the south and several bays to the north (Fig. 1). Habitat types in the study area consisted of ocean-front sandy beaches, dunes, overwashes (areas where storm water carried sand landward over the island), bay-side sandy beaches, ephemeral pools, and filled island breaches originally formed by Hurricane Sandy (Walker et al. 2019). The study area also included three inlets, Fire Island Inlet, Old Inlet and Moriches Inlet. Hurricane Sandy storm surges formed Old Inlet. Fire Island and

Moriches inlets are dredged inlets, stabilized with jetties to the east and west. Two restoration areas were built by the U.S. Army Corps of Engineers (USACE) prior to the 2015 plover breeding season to mitigate for island stabilization efforts, one at the eastern end of Smith Point County Park (Great Gun, 34.8 ha), and one in the middle of Smith Point County Park (New Made, 6.6ha; Bellman 2018, Walker et al. 2019). Human use was variable among management areas and comprised pedestrian and off-road vehicle use, with boat access along the shoreline (DeRose-Wilson et al. 2018). Dominant vegetation included American beachgrass (*Ammophila breviligulata*), common reed (*Phragmites australis*), seaside goldenrod (*Solidago sempervirens*), and wooly beachheather (*Hudsonia tomentosa*). Fire Island also supports both coniferous and deciduous tree communities, and poison ivy (*Toxicodendron radicans*) thickets, but these were not within plover breeding areas.

Field methods

We surveyed beaches for plovers April–August during 2016–2018 (DeRose-Wilson et al. 2018, Walker et al. 2019, Weithman et al. 2019). We searched for nests using behavioral cues and by grid-searching plover habitat. We trapped adults at nests using drop-traps and banded adults using either uniquely identifiable 4-color band combinations on the tibiotarsus or a uniquely coded alphanumeric flag opposite a color band on the tibiotarsus. We confirmed adult plovers as breeders by trapping them on nests or by confirming incubation using 20–60x spotting scopes.

We surveyed for banded adults and chicks every 1–3 days by walking transects parallel to the shoreline through subsites assigned by geomorphic features (i.e., overwash, backshore, restoration area). Upon observation of individuals, we assigned a behavior to each individual based on observed behavior at first encounter and later clustered all behaviors into two categories: parental and non-parental. Parental behaviors included broken wing displays, defensive peeping, and brooding, whereas non-parental behaviors included foraging, aggressive,

or territorial behaviors, roosting, loafing, and courtship. We also recorded disturbed as a behavior, indicating displacement prior to initial observation. We omitted disturbed locations from analyses because they were not initial behaviors. We recorded individual locations of birds with coordinate geometry by first collecting an observer's location using a Trimble GPS unit (Trimble Geospatial, Sunnyvale, CA, USA), and offsetting that location with an azimuth from a compass and a distance from a Nikon 8397 Aculon Laser Rangefinder (Nikon, Minato, Tokyo, Japan; Robinson et al. 2020).

We monitored nests until hatch or failure and monitored all broods until fledge or failure. We estimated nest initiation date assuming 1.5 days to lay each egg (Wilcox 1959, Haig and Oring 1988). If a nest was found at four eggs or remained at the initial egg count for four nest visits, we floated eggs to estimate initiation date (Westerskov 1950). We considered chicks fledged at 25-days post-hatch.

Adult movement

To determine potential scales that adult plovers selected habitat variables, we used plover movement data to define radii of circles within which we summarized habitat data. We estimated the average and median distance that individuals moved within a day using all observations where we collected $\geq$ one location of an individual within a day. We also estimated the average and median distance between subsequent daily observations. Finally, using birds in the nesting stage, we estimated the mean distance birds were observed from their nest. Because no prior knowledge is known about selection scale in adult plovers, we used all potential movement values as circle radii, to not rule out any potential scale relationships. The minimum scales used were 5m and 10m, the mean and maximum error in the location data collection (Robinson et al. 2020).

Image classification

Imagery and LiDAR were flown by aircraft between February and April, 2016–2018 (Axis Geospatial, Easton, MD, USA). We classified fine-scale (15 cm) imagery for each year into four classes (dry sand, wet sand, vegetation, and water), using Maximum Likelihood Classification in ArcGIS 10.6 (ESRI Inc., Redlands, CA, USA). We manually interpreted and digitized development in our study area (i.e., parking lots, jetties, boardwalks), and incorporated development into the classification as a fifth landcover class. We also had LiDAR flown for each year, from which we created a digital elevation model (DEM). As the timing of aerial imagery did not always correspond with low tide, we used the DEM to identify intertidal areas. The oceanfront intertidal range was 0–1.2 m in elevation, based on the Astronomical High Water at NOAA Moriches Inlet tidal station, and the bayside intertidal range was 0–44.50 cm, based on mean high water at the NOAA Smith Point Bridge tidal station (NOAA 2017). We reclassified each DEM to select pixels within both the oceanfront and bayside intertidal and subtidal range. These pixels were reclassified to represent intertidal wet sand and water, respectively. The refined layers from each of these methods were superimposed over the classification.

Variables

We created several 1-m raster layers using the landcover classifications to evaluate specific hypotheses. To understand selection for foraging habitat, we created raster layers for Euclidean distance to ocean, Euclidean distance to bay, least cost distance to ocean, and least cost distance to bay. We also created layers for Euclidean distance to development and Euclidean distance to vegetation that we hypothesized would represent selection for habitat that reduced predation risk as vegetation can conceal terrestrial predators. Development in the study area, in addition to representing human disturbance, could represent areas that avian and mammalian predator species congregate in search of anthropogenic waste as food and generally included roads,

parking lots, buildings, and constructed jetties. Potential predators of plovers that may be influenced by development or vegetation include avian predators such as herring gull (*Larus argentatus*), great black-backed gull (*L. marinus*), American crow (*Corvus brachyrhynchos*), and fish crow (*C. ossifragus*), whereas mammalian predators included red fox (*Vulpes vulpes*), raccoon (*Procyon lotor*), and feral cat (*Felis catus*). For distance rasters each pixel in a raster had a single value that represented the distance from that cell to a landscape feature of interest. Least cost distance rasters represented the minimum walking distance to a feature assuming water and vegetation are movement barriers (Walker et al. 2019). We created Euclidean distance layers using the Euclidean Distance tool in ArcGIS and least cost distance layers using the Path Distance tool. We used the DEM to evaluate selection for elevation. High elevation areas may increase susceptibility to aerial predators due to improved detectability of predatory birds in flight. High elevation areas also are more likely to be dry, and thus have lower invertebrate abundance. Finally, we derived a slope layer from the DEM, using the Slope tool in ArcGIS, hypothesizing that steeper area would be selected against by adults, as steeper areas also may have lower marine invertebrate abundance.

We generated five times as many random points as used points to represent available habitat for plovers (Cooper and Millspaugh 2001). Because detection probability of plovers is likely low in vegetation, and the plovers primarily use sandy habitats, we constrained used and random points to wet and dry sand pixels. Within circles with radii of each potential selection scale, we averaged all values of each variable for the adult plover locations and random locations using the ‘extract’ function in the *raster* package in R (Hijmans 2016, R Core Team 2018). In each circle, we also calculated the proportion of dry sand and vegetation pixels, as areas with more dry sand and less vegetation are likely to reduce plover detection by predators. To compare

effect sizes among predictor variables, we scaled all continuous variables using the mean and standard deviation.

Scale optimization

As habitat selection is a multi-scale process and each landscape feature may be evaluated by plovers at different scales, we used scale optimization to determine the most relevant scale at which adult plovers selected each variable. We developed separate model sets for each landscape variable. In a model set, each scale identified by the adult movement analysis was a predictor variable in univariate resource selection functions (Chambers et al. 2016, McGarigal et al. 2016). We ranked each model in a set by AICc, selecting the best-supported scale with ≤ 2 AICc. If there was not one clearly supported scale, we selected the smallest scale with ≤ 2 AICc based on adult plovers being relatively small, thus likely making choices at fine scales (Miguet et al. 2016). We tested for correlation among the final set of predictors at their selected scales. To reduce spatial autocorrelation, we spatially rarified the data by removing locations in each breeding stage, year, and type of point (used or random) within 5m of all other points using the SDMtoolbox for ArcGIS 10.6 (Brown et al. 2017).

Analytical methods

We evaluated second-order selection of adult piping plovers in the study area on Fire Island and Westhampton Island, New York (Fig. 1). We randomly subset our adult locations and random points into a training set (75%) and a testing set (25%) to evaluate the accuracy of our predicted model. All RSF models were built using the training set. Based on our hypotheses of whether behavior or breeding stage better explained adult habitat selection, we assigned each adult location a breeding stage and behavior for three categorical predictor groups.

The first grouping classified adults by breeding stage; pre-breeding, nesting, brooding, and post-breeding. Adults were nesting if observed between the time of nest initiation and nest

hatch or failure. Adults were brooding if observed between nest hatch and the last time a brood was observed alive or 25-days post-hatch. If observed prior to nest initiation or following nest failure, brood failure, or brood fledging, we categorized adults as pre-breeding and post-breeding, respectively. If an individual nested more than once, we removed locations between nesting attempts. Adults during this period may exhibit different habitat selection, but we did not have a sufficient sample from this stage.

As nest site selection may influence brood-site selection, we also simplified this classification into ‘simple breeding stage’ with two classes for a second grouping; adults in nesting and brooding stages were combined into a ‘breeding’ class and pre- and post-breeding stages were combined for a ‘non-breeding’ class. The final, third classification split adults by instantaneous behavioral differences, birds that were in a breeding stage and exhibiting parental behavior (parental) and all other adults (non-parental). For an adult to be in the parental behavior class, they needed to be in a breeding stage, and also be exhibiting parental behaviors. For an adult to be in the non-parental behavior class, they could either be in one of the non-breeding stages or be in a parental breeding stage and exhibiting behaviors that are not classified as parental (see Field methods). We then used the categorical predictors of behavior or breeding stage in resource selection functions.

We evaluated fixed effects logistic regression models with additive or interactive effects of all our predictor variables at the best-supported scale, with either adult breeding stage, simple breeding stage, or behavior class, and year. We evaluated all models against a base model that included all landscape variables but did not include year, breeding stage, or behavioral class. The model set included 15 models, and we ranked models using AICc. We considered all models ≤ 2 Δ AICc to be competitive (Burnham and Anderson 2002). We evaluated resource selection and

habitat suitability based on the adult grouping (i.e., breeding stage, simple breeding stage, behavior) in the best supported model.

Creation of suitable habitat layer

We used Focal Statistics, a moving window analysis tool, in ArcGIS to create raster layers representing the best supported scale for each year. The resulting rasters were 1-m resolution, but each cell represented the average value or landcover proportion within a circle with a variable-specific scale radius. We scaled each predictor raster to the mean and standard deviation of the used and random point data and only retained cells that were dry or wet sand from the landcover classification because adult and random points were constrained to wet and dry sand. We used Raster Calculator in ArcGIS to visualize the best supported RSF model. We created a visualization for each year, and as many unique classes in the top resource selection model, using year-specific raster layers.

We validated predicted habitat suitability using the 25% of used and random points excluded from model development. We divided the predicted RSF surface into 5- and 10- equal-area visualization classes, where each visualization class was the range of probability values that allowed for an equal number of pixels among all classes (Boyce et al. 2002, Morris et al. 2016). The first class would represent the 10 or 20% of pixels with the lowest predicted suitability range, and the fifth or tenth class would represent the 10 or 20% of pixels with the highest predicted suitability. We then extracted the class number to each plover use point in the training set. We evaluated model fit by correlating class number with the proportion of training points in each bin (Boyce et al. 2002). For visualization, we selected the number of visualization classes (5 or 10) which resulted in the highest correlation over the most year-group combinations.

To evaluate the total amount of suitable habitat, we determined a suitability threshold for each year-class combination using the minimized difference threshold (MDT; Jiménez-Valverde

et al. 2013), where the difference between sensitivity (true positive rate) and specificity (true negative rate) is calculated for each possible suitability threshold (1–100). The cutoff value that represents the smallest difference between sensitivity and specificity is the selected threshold. Using this value, any predicted suitability value on the predicted raster above the threshold would be suitable, and any value below the threshold would be unsuitable. We used the 25% training point subset to evaluate how well the suitability layer predicted adult plover use points by determining the proportion of plover points in suitable habitat. Finally, we summed the predicted suitability layers from each year for an ensemble layer to visualize where habitat suitability agreed or differed between or among the best supported grouping scheme.

Results

We recorded 2,889 adult locations during 2016–2018 from 172 breeding individuals. After assuring a minimum of 5-m between locations within location type, year, and breeding stage, we had 2,060 adult plover observations. Of these locations, 19.9% were pre-breeding, 40.2% were nesting, 29.4% were brooding, and 10.5% were post-breeding. For the behavior class, 42.1% were breeding and exhibiting parental behaviors and 57.9% were exhibiting non-parental behaviors.

Adult movement

For the locations of adult plovers where the time between subsequent observations was one day ($N = 309$), adults moved on average 344 m ($SE = 53$; median = 106). For locations where we collected subsequent observations of individuals on the same day, adults moved on average 211 m ($SE = 20.95$) with a median of 87 m. Adult plovers with active nests were observed 150 m ($SE = 11$) from their nest, on average.

Selection scales

Based on these movement distances, we used seven circle sizes in which to evaluate selection for different habitat attributes (Table 1). Generally, larger scales were better representations of plover selection; however, slope, dry sand proportion, and vegetation proportion were represented at scales < 100m (Table 1, Tables E1–E10). Despite being evaluated at different scales, Euclidean and least cost distance to ocean intertidal and Euclidean and least cost distance to bay were correlated ($r = 0.79$ and 0.84 , respectively). We continued modeling efforts with the two least cost distance variables because, although we were modeling adults that could fly and thus could reasonably reach any pixel of ocean or bay intertidal, adults tending broods were limited by habitat availability for their chicks and were unlikely to fly to areas their chicks could not access.

Resource selection

A single model, the interactive model in which habitat selection was best described by behavioral group (parental vs. non-parental), but not by year, held 85% of the weight in model selection (Table 2). Nearly all landcover variables were influential to plover habitat selection (Fig. 2, Table D1).

Plovers in both parental and non-parental behavior classes avoided areas with more vegetation, but they selected sites at lower grades and areas closer to ocean intertidal habitat (Figure 3). Selection differed between the behavioral phases, such that non-parental plovers avoided areas with greater proportions of dry sand relative to random points, whereas parental plovers selected areas with higher proportions of dry sand (Figure 4). Parental plovers selected for areas at higher elevation than non-parental plovers, but overall, lower elevations were favored compared to random points for both behavioral groups (Figure 4). Parental plovers also

selected areas closer to the bay intertidal whereas non-parental adult plovers did not select habitat relative to the distance to bay intertidal (Figure 4). Birds in both behavior classes also selected for sites farther from development, although the magnitude of the effect was greater for non-parental adults.

Mapping

The mapping schemes that used 5 equal-area visualization classes were more predictive than 10 equal-area visualization classes for every predictive raster made. Predictive accuracy with 5 visualization classes using our 25% training sample ranged from 0.75–0.93 (Table 3).

Binary suitability thresholds (suitable vs not suitable), as determined by the minimized difference threshold (MDT) ranged from 0.18–0.19. Therefore, predicted suitability below 0.18 – 0.19 was considered unsuitable, and above was considered suitable. There was more suitable habitat in each year for parental adults (28–34% of sand) than non-parental birds (22–23% of sand) when using the specific class and year suitability threshold for each visualization of the selection results (Table 3). Suitable habitat only encompassed 60–72% of the adult parental used points and 66–73% of the adult non-parental used points, suggesting the model was predicting some habitat adults used to be unsuitable (Table 3). The amount of suitable habitat ranged from 100.14 ha to 151.07 ha, declined an estimated 21.5 ha for parental plovers between 2016 and 2018, and increased an estimated 8.5 ha for non-parental plovers between 2016 and 2018.

Visually, areas overwashed by Hurricane Sandy were consistently mapped as suitable habitat. Overwashes had large patches of dry sand reaching from the ocean to the bay, and access to both ocean and bay intertidal habitat. Other suitable areas included one of the built restoration areas (Fig. 5), and the area around the inlet created by Hurricane Sandy. Generally, intertidal habitats were more suitable for non-parental plovers than parental plovers (Figure 5). Sandy backshore areas, between the ocean intertidal and the primary dune, mapped as more suitable for

parental plovers than non-parental plovers. The larger USACE restoration area mapped as highly suitable for parental plovers and less suitable for non-parental plovers. From the ensemble layer of the two behavioral classes for each year, 16.1–19.6% of the sand in the study area was suitable for at least one behavioral class, and 17.1–19.1% was suitable for both behavioral classes (Figure 6).

Discussion

Habitat selection of adult piping plovers, apart from their nest sites, has rarely been assessed, and to our knowledge, has never been assessed using spatially explicit locations of individual adults. For several habitat variables, parental adult plovers selected habitat differently than non-parental plovers. Furthermore, on Fire Island and Westhampton Island there was more suitable habitat for parental plovers than for plovers exhibiting other behaviors. This divide in selection demonstrates that we should not only evaluate habitat suitability using stationary or spatially implicit data, but instead we should consider habitat needs across life stages for a holistic assessment of habitat needs.

The strongest predictor of habitat selection for both behavioral states was the amount of vegetation within 10m of sand pixels. Probability of use was nearly zero at 50% vegetation cover. Determining use thresholds and identifying avoidance of certain sized vegetative patches, can assist managers to design or modify landscapes to best suit the habitat needs of species (Huggett 2005). Therefore, this may be a threshold at which vegetation becomes too dense for plovers to move through and becomes a liability for predator detection and concealment. Past studies illustrated that plovers readily use sparsely vegetated habitats, even occasionally placing their nest right next to, roosting under, or gleaning insects off of vegetation (Burger 1987, McGowan et al. 2007, Cohen et al. 2008b). Use of sparsely vegetated habitat also was supported

by the lack of avoidance for areas close to vegetation in parental plovers. Fifty percent vegetation within 10m would represent a 160m² patch of vegetation, or multiple patches totaling 160m². Managers could use this level of vegetation as a target size to remove vegetation patches in nesting plover areas, or when vegetation is more than sparse.

Similarities in selection between behavioral stages also were apparent for slope and least cost distance to ocean intertidal. Selection for areas closer to the ocean intertidal and areas of lower slope, both likely represent the importance of foraging habitat for adult plovers (Fraser et al. 2005, Cohen et al. 2009). If, for example, a particular area is close to the ocean, but the slope is steep, it may not have as abundant or accessible marine invertebrate prey that plovers probe for in the sandy intertidal zone (Jaramillo et al. 1993).

Avoidance of areas that have less vegetation around them likely represents predator avoidance for plovers. Similarly, avoidance of developed areas such as parking lots or buildings may reflect strategies to avoid predators, which may be attracted to human food at waste disposal sites. Avoidance of development also could be a strategy to reduce exposure to human disturbance. Anthropogenic disturbance was negatively correlated with plover chick survival (DeRose-Wilson et al. 2018) and adult survival (Gibson et al. 2018). While both behavioral stages avoided development in our study, the magnitude of development avoidance was greater for non-parental adults than parental adults. This difference may be related to specific sites selected by post-nesting birds, particularly the areas surrounding the new inlet created by Hurricane Sandy that supported approx. 30% of adult post-nesting locations. The new inlet (Old Inlet; Fig. 1) is part of the National Wilderness Preservation System (Dietz et al. 2015), which reduces or eliminates human and vehicle traffic, and is about 2km from the nearest human

development. Thus, it may be attractive to plovers trying to fuel up for migration without being disturbed.

A lack of selection for bay intertidal habitats by non-parental behavior plovers was surprising. Bay intertidal habitats tend to have greater invertebrate abundance than ocean intertidal habitats (Loefering and Fraser 1995, Cohen et al. 2009, DeRose-Wilson et al. 2018), and many non-parental birds exhibited foraging behaviors (approx. 40%). However, adults in the non-breeding period tended to congregate near the inlet created by Hurricane Sandy (approx. 30%), and the eastern side did not have access to low-intertidal bayside foraging habitat. Instead, the inlet and ocean intertidal habitats accreted following Hurricane Sandy as the land surrounding the inlet began to migrate. Consequently, foraging quality in these areas may have been similar to some bay areas. This site also is adjacent to disconnected flood shoals, submerged sandbars that emerge at low tides, which were not included in our analysis. Non-parental adults, particularly post-breeding, foraged at flood shoals at low tide and roosted around the inlet at high tide (S. Robinson, personal observation).

On average, non-parental adults were about 400m farther from the bay compared to parental adults, potentially because parental adults preferred to bring their chicks to the bayside foraging areas. Piping plovers are highly territorial (Elliot-Smith and Haig 2004), so if parental adults were including bayside foraging habitats in territorial boundaries, they may have forced non-parental adults to forage elsewhere. Further, post-breeding birds were observed at similar distances to bay intertidal habitat as birds exhibiting parental behaviors, suggesting that this possible territorial avoidance was released once chicks fledged. Despite this apparent difference, the effect size of selection for bayside intertidal habitat was small relative to other habitat

variables. Therefore, other features of the landscape drove selection more than bayside habitat, such as vegetation.

There was more suitable habitat on Fire Island and Westhampton Island for parental plovers than non-parental plovers. Fire Island is not a known hot spot for migration for plovers or other shorebird species. While the island does get some north and southward migrants from other breeding areas, such as Atlantic Canada, there are far more important stopover areas in the Atlantic plover range during migration (Weithman et al. 2018). Instead, in the years of this study, Fire Island was a highly productive breeding site with high reproductive output and immigration of breeding birds (Chapter 2), and the breeding population exponentially increased following Hurricane Sandy (Walker et al. 2019, Weithman et al. 2019). To increase the suitability of habitat for non-parental birds, managers should enhance protection of habitats that non-parental adults selected, primarily oceanside foraging habitats, which during much of the breeding season on our study site were occluded by human disturbance from vehicular and human traffic (Walker et al. 2019).

Using the predicted habitat suitability maps for piping plovers on Fire and Westhampton islands, we can begin to target areas that could serve as future habitat restoration sites. As vegetation proportion was the most influential selection predictor, it is important to focus future plover habitat management plans on reducing vegetation cover, particularly within large parcels of dry sand. Vegetation cover is easily modifiable due to widespread availability of both mechanical and chemical vegetation removal options (Powell and Collier 2000, Cohen 2005). Although important to parental adult plovers, bay intertidal habitat is a challenging feature on the landscape to create without significantly altering the geomorphic quality of the landscape or annual vegetation management. However, allowing storms like Hurricane Sandy to alter the

island as it would naturally can increase the overall amount of bayside intertidal habitat for plovers (Cohen et al. 2009, Walker et al. 2019). Prior to Hurricane Sandy, unvegetated bay intertidal was limited in our study area. Following Hurricane Sandy, overwash areas were among the most suitable areas for adult plovers, demonstrating the plastic nature of these birds. Furthermore, because plovers are still selecting for Hurricane-created habitat six years after the storm illustrates the long-term benefits of natural processes. The protection of intertidal habitats also benefits other migratory shorebirds, such as the federally threatened *rufa* red knot (Monk et al. *in revision*) and may be increasingly necessary with the accelerating loss of intertidal wetlands and climate change (Iwamura et al. 2013, Davidson 2014).

Nest site selection studies generally agree with what parental adults exhibited, but disagree with non-parental adult selection in some cases. Further, we did not consider microhabitat selection (Cohen et al. 2008b, Grant et al. 2019). Similar to what has been found for nest site selection, adults of both behavioral classes were selecting for areas at lower elevation (Maslo et al. 2011). In this study, we included evaluation of intertidal areas that were unavailable for nesting. These intertidal areas were the most suitable to non-parental plovers, demonstrating the divide between nest site selection and adult habitat selection. Other plovers also display similar selection patterns as piping plovers, for example, snowy plovers select for wide beaches that are less sloped (Leja 2015). Kentish plovers (*Charadrius alexandrinus*) select nest sites with higher visibility, which was hypothesized to improve the ability to detect predators, and avoided human disturbance (Gómez-Serrano and López-López 2014).

As this study did not entirely align with nest-site selection studies, habitat evaluation should not just consider the placement of nests, but also must consider habitat needs of other plover life stages. This need for a broader focus of habitat management is similar to what was

suggested for the Great Plains population, that only focusing on nesting habitat can be detrimental to piping plover chicks by creating an ecological trap (Wiltermuth et al. 2015), and we propose that the same is true for adult piping plovers on the Atlantic Coast. Continuing to study the life stages of plovers that move across the landscape can lend insight into whether behavioral habitat selection differs among populations or within smaller geographic areas. Future work on this issue could focus on chick habitat selection in this novel post-storm landscape to see if further differences exist between pre-fledged broods and adults and whether selection relationships track survival relationships and or species persistence.

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Environmental Conservation Endangered Species permit #314, New York State Office of Parks, Recreation and Historic Preservation permits 16–0393, 17–0755, 18–0168 and permits for Research in Suffolk County Parklands.

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Tables

Table 1. Potential scales tested for resource selection of habitat by adult piping plovers on Fire and Westhampton islands, NY, 2016–2018. Scales were evaluated for each landscape variable and ranked by AICc in univariate logistic regression models (Appendix S1).

Potential resource selection scale (m)	Source of scale	Variables best supported at scale
		Distance to bay intertidal, dry sand
5	Mean location error [†]	proportion
10	Maximum location error [†]	Vegetation proportion
	Median distance between subsequent adult	
87	locations within a day	-
	Median distance between daily adult	
106	locations	Elevation, distance to vegetation
	Mean distance nesting adults observed from	
150	their nest	-
	Median distance between subsequent adult	
211	locations within a day	Least cost distance to bay intertidal
		Distance to ocean intertidal, least cost
344	Mean distance between daily adult locations	distance to ocean intertidal

[†] Robinson et al. 2020

Table 2. Model selection table to assess differences in resource selection for adult piping plovers between class and year. Breeding stage indicates that adult locations were split into four classes, pre-breeding, nesting, brooding and post-breeding. Simple breeding stage indicates that adult locations were split into two classes based on whether adults were breeding (nesting or brooding) or not (pre- or post-nesting). Behavior indicates that adult locations were split into two classes based only on behavior, parental and non-parental. Predictors included elevation, slope, least cost distance to ocean intertidal, least cost distance to bay intertidal, distance to vegetation, distance to development, proportion of sand around points and proportion of vegetation around points.

Model	K [†]	ΔAICc	w _i [‡]	Log likelihood
Predictors * Behavior	18	0.00	0.85	-3898.07
Predictors * Behavior * Year	54	3.42	0.15	-3863.53
Predictors * Breeding Stage	36	50.05	0.00	-3905.00
Predictors * Simple Breeding Stage	18	66.52	0.00	-3931.33
Predictors * Breeding Stage * Year	108	67.59	0.00	-3840.75
Predictors * Simple Breeding Stage * Year	54	69.13	0.00	-3896.38
Predictors * Year	27	74.13	0.00	-3926.09
Predictors + Simple Breeding Stage + Year	12	76.92	0.00	-3942.55
Predictors + Year	11	77.95	0.00	-3944.07
Predictors + Behavior + Year	12	78.68	0.00	-3943.43

Predictors + Breeding Stage +				
Year	14	79.46	0.00	-3941.81
Predictors + Simple Breeding				
Stage	10	82.14	0.00	-3947.16
Predictors	9	83.01	0.00	-3948.60
Predictors + Breeding Stage	12	83.52	0.00	-3945.85
Predictors + Behavior	10	83.93	0.00	-3948.06
† Number of parameters ‡ Model Weight				

Table 3. Proportion of suitable habitat and total suitable hectares across two behavioral classes from 2016–2018 as predicted by a resource-selection function model assessing adult piping plover habitat selection.

Behavior class	Year	Proportion habitat suitable	Hectares suitable habitat	5-bin correlation	10-bin correlation	Proportion used points suitable
Parental	2016	0.34	151.07	0.89	0.85	0.68
Non-parental	2016	0.22	100.14	0.83	0.75	0.73
Parental	2017	0.34	149.57	0.9	0.82	0.60
Non-parental	2017	0.23	100.66	0.88	0.84	0.67
Parental	2018	0.28	129.57	0.93	0.85	0.72
Non-parental	2018	0.23	108.83	0.88	0.85	0.66

Figures

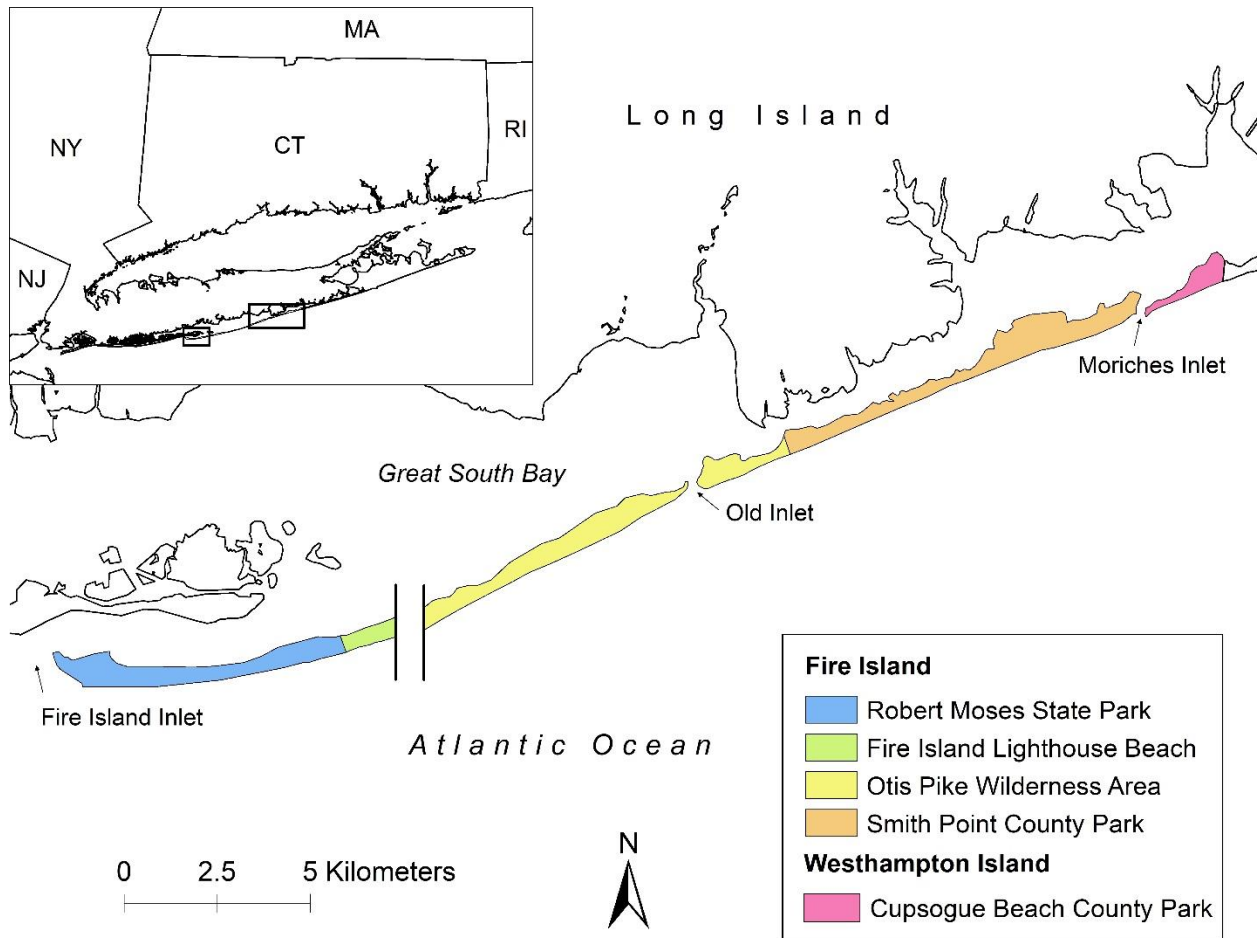


Figure 1. Study area in which adult plover locations were located during 2016–2018 and resource selection functions created to understand habitat selection of adult plovers between breeding stages or behavior classes.

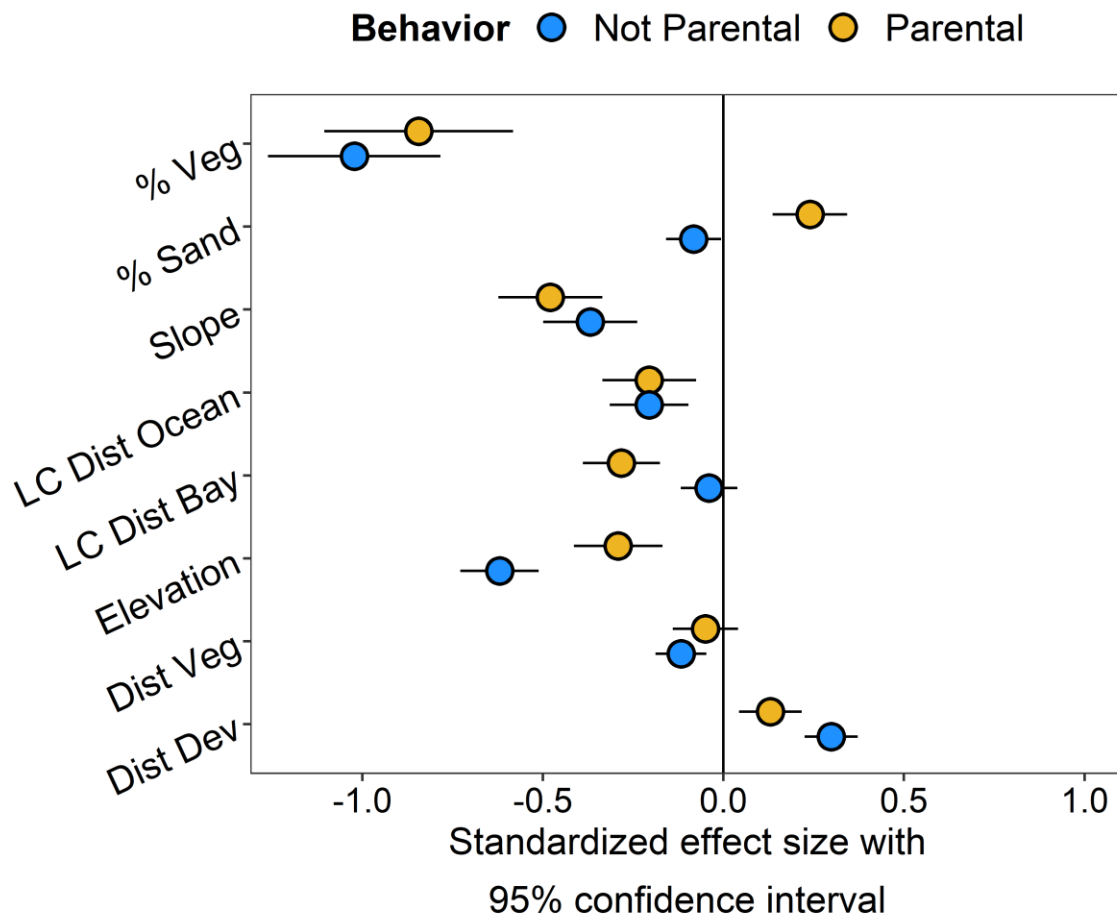


Figure 2. Standardized effect size for top ranked logistic regression resource selection function describing breeding adult piping plover habitat selection on Fire Island, New York. For distance variable, a negative effect suggests selection closer to the feature and for proportion variables, a positive effect suggests selection with more of the feature within the specified buffer.

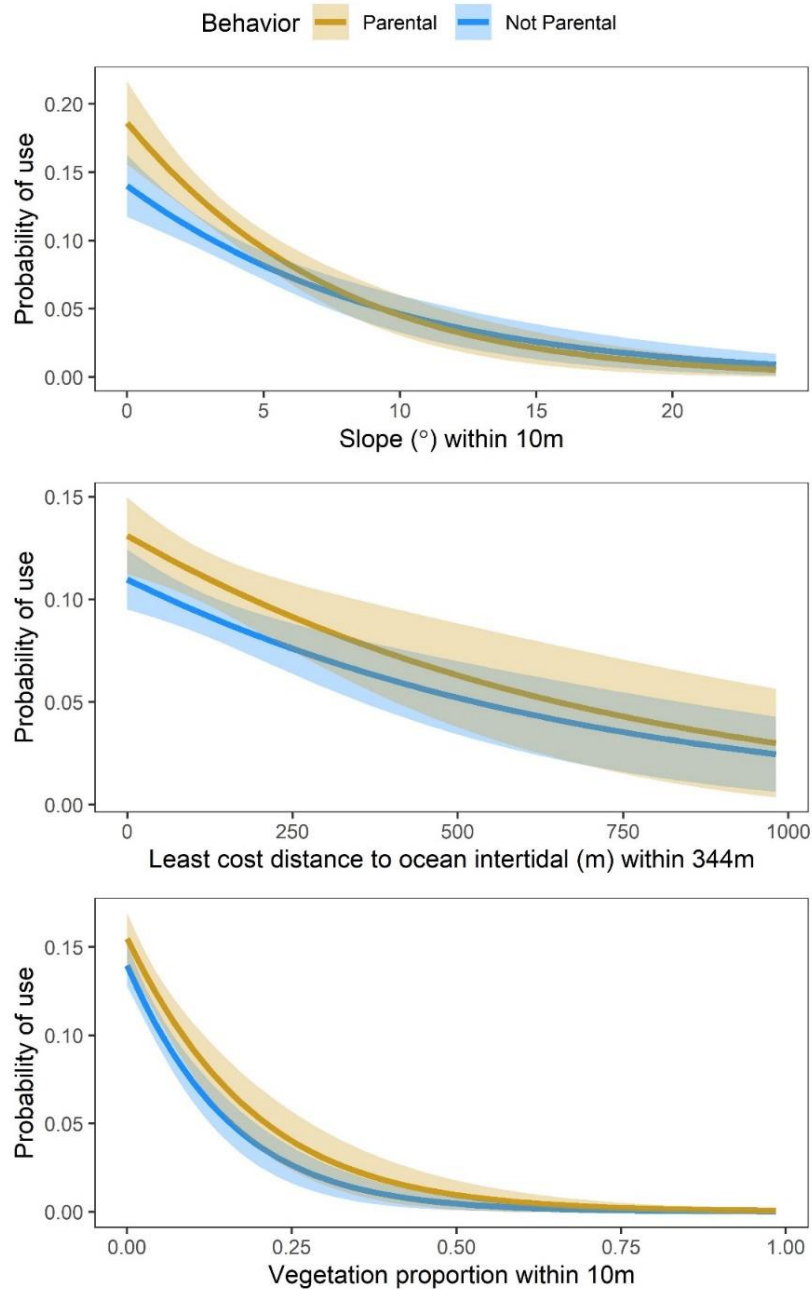


Figure 3. Three variables from a logistic regression resource selection function, assessing habitat selection of adult piping plovers on Fire Island, NY, which signified similar relationships between adults behaving parentally and adults exhibiting all other behaviors. Lines are predicted response with all other variables in the model set to the mean.

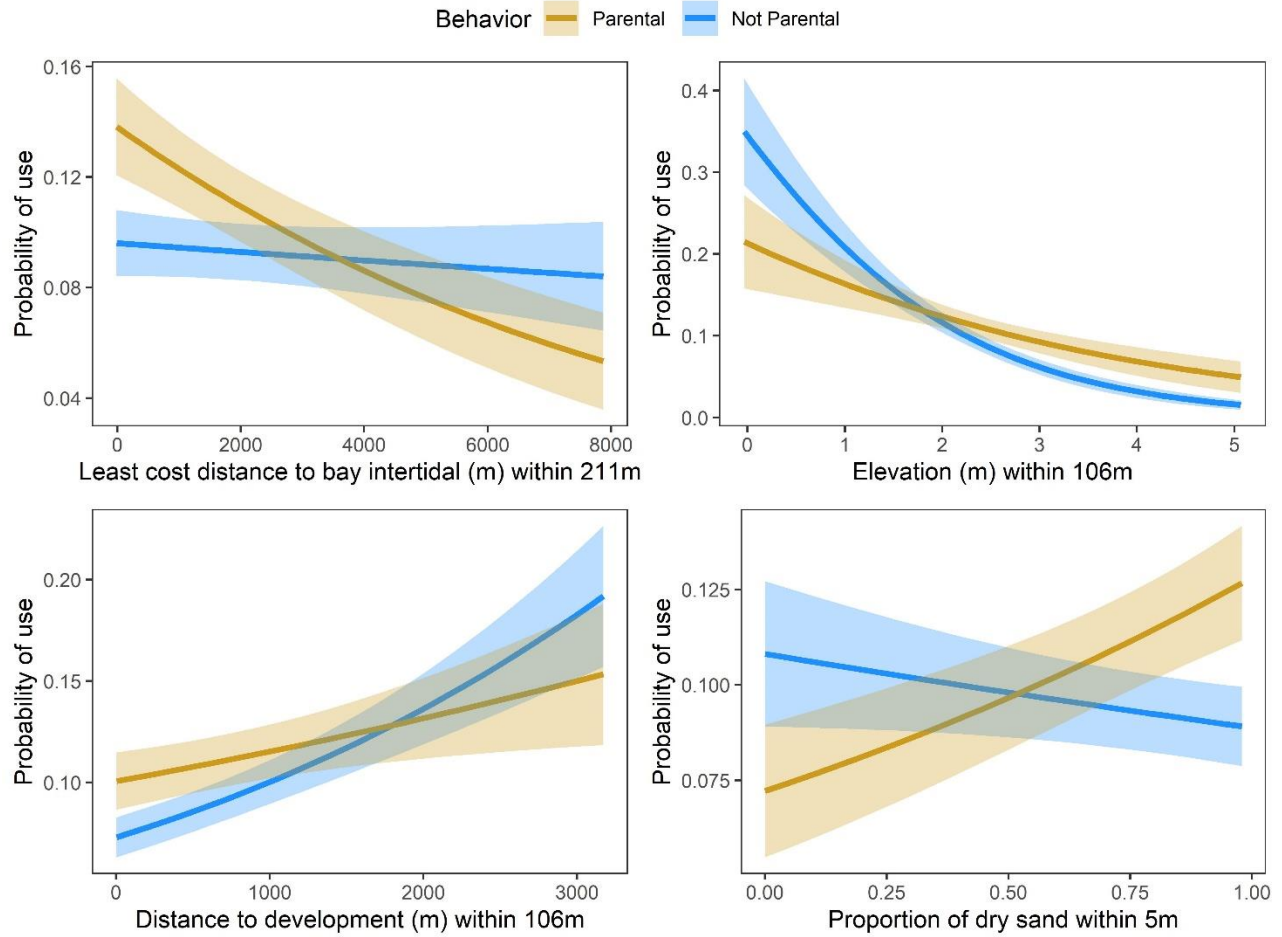


Figure 4. Four variables from a logistic regression resource selection function, assessing habitat selection of adult piping plovers on Fire Island, NY, which signified differences between adults behaving parentally and adults exhibiting all other behaviors. Lines are predicted response with all other variables in the model set to the mean.

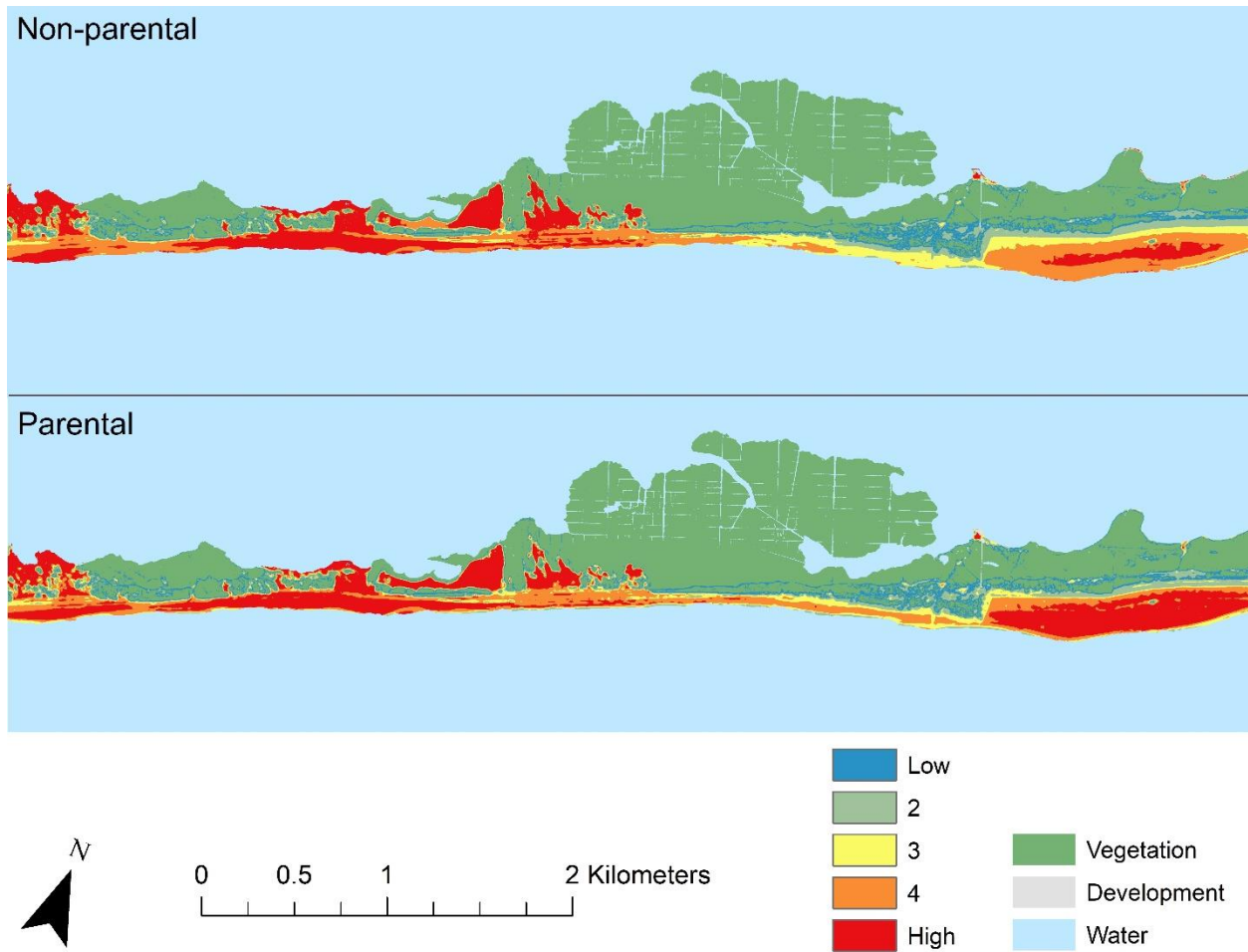


Figure 5. Predicted habitat suitability maps for adult piping plovers on Fire Island, New York exhibiting non-parental behavior (top) and parental behavior (bottom). Resource selection function predicted onto 2016 aerial imagery and landcover classifications. The right-most area on the figure represents a restoration area built for piping plover nesting habitat prior to the 2015 breeding season.

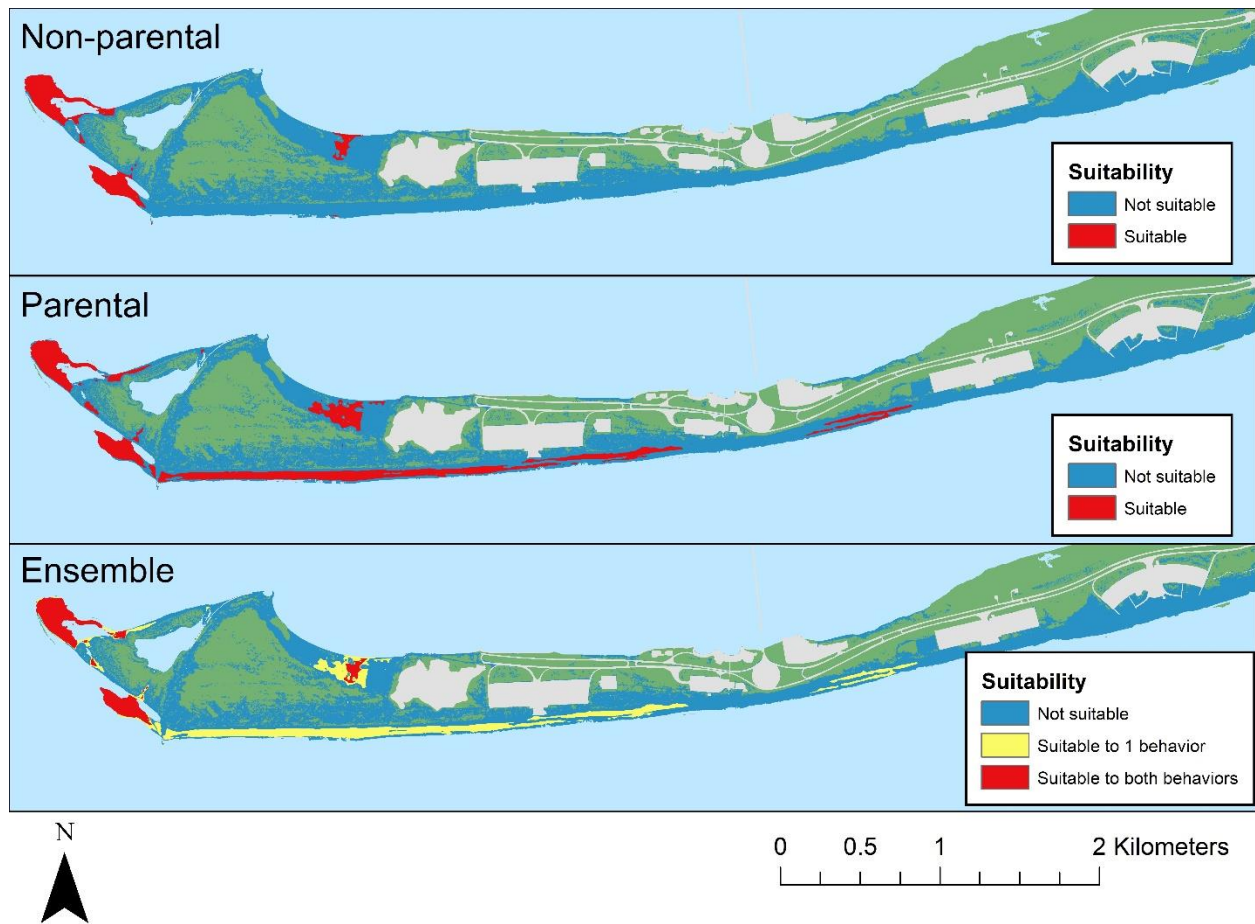


Figure 6. Suitable versus non-suitable sand for non-parental plovers (top), parental plovers (middle) and an ensemble of both non-parental and parental plovers (bottom). Resource selection function predicted onto 2016 aerial imagery and landcover classifications.

Appendix D. Means for resource selection predictor variables.

Table D1. Mean variables with SE and top scale for the top-selected grouping variable in a resource-selection function model assessing adult piping plover habitat selection based on behavior.

Variable	Scale (m)	Mean Parental (SE)	Mean Non- parental (SE)	Mean Random (SE)
Elevation (m)	106	2.20 (0.025)	1.78 (0.021)	2.43 (0.0082)
Slope (°)	10	2.55 (0.074)	2.20 (0.050)	4.07 (0.029)
Distance to vegetation (m)	106	26.09 (1.04)	29.36 (0.95)	20.59 (0.25)
Distance to ocean intertidal (m)	344	131.79 (1.98)	118.65 (1.78)	163.49 (0.84)
Distance to bay intertidal (m)	5	565.58 (22.14)	526.18 (16.61)	1278.92 (15.28)
Distance to development (m)	106	950.92 (29.32)	1210.56 (23.01)	708.15 (7.66)
Least cost distance to ocean intertidal (m)	344	100.78 (2.14)	96.86 (2.32)	115.22 (1.24)
Least cost distance to bay intertidal (m)	211	1391.29 (64.59)	1701.01 (64.56)	1869.46 (19.62)
Dry Sand proportion (m)	5	0.81 (0.013)	0.60 (0.013)	0.77 (0.0033)
Vegetation proportion (m)	10	0.013 (0.0017)	0.012 (0.0015)	0.073 (0.0014)

Appendix E. Scale optimization model sets

Table E1. Scale optimization model set for dry sand proportion around piping plover adult used and random points.

Dry Sand Proportion				
Model	$K^\dagger$	$\Delta AICc$	$w_i^\ddagger$	Log likelihood
5	2	0.00	1	-5966.56
211	2	28.44	0	-5980.78
10	2	30.20	0	-5981.66
150	2	40.07	0	-5986.60
344	2	44.02	0	-5988.57
106	2	63.79	0	-5998.46
87	2	71.59	0	-6002.36
Null	1	73.94	0	-6004.53

Table E2. Scale optimization model set for vegetation proportion around piping plover used and random points.

Vegetation Proportion				
Model	$K^\dagger$	$\Delta AICc$	$w_i^\ddagger$	Log likelihood
10	2	0.00	0.88	-5713.19
87	2	3.92	0.12	-5715.15
106	2	27.27	0	-5726.83
150	2	49.49	0	-5737.94
344	2	55.87	0	-5741.13

211	2	85.21	0	-5755.80
5	2	137.21	0	-5781.80
Null	1	580.68	0	-6004.53

Table E3. Scale optimization model set for Euclidean distance to bay (m) around piping plover adult used and random points.

Euclidean Distance to Bay				
Model	$K^\dagger$	$\Delta AICc$	$w_i^\ddagger$	Log likelihood
5	2	0.00	0.42	-6128.12
10	2	0.10	0.40	-6128.16
87	2	3.10	0.09	-6129.66
106	2	3.87	0.06	-6130.05
150	2	5.77	0.02	-6131.00
211	2	8.75	0.01	-6132.49
344	2	15.33	0	-6135.78
Null	1	620.61	0	-6439.42

Table E4. Scale optimization model set for Euclidean distance to ocean intertidal (m) around piping plover adult used and random points.

Euclidean Distance to Ocean Intertidal				
Model	$K^\dagger$	$\Delta AICc$	$w_i^\ddagger$	Log likelihood
344	2	0	1	-6170.38
211	2	285.46	0	-6313.11

150	2	386.47	0	-6363.61
106	2	428.68	0	-6384.72
87	2	441.05	0	-6390.90
10	2	466.54	0	-6403.65
5	2	466.87	0	-6403.81
Null	1	536.09	0	-6439.42

Table E5. Scale optimization model set for least cost distance to ocean (m) around piping plover adult used and random points.

Least Cost Distance to Ocean				
Model	$K^{\dagger}$	$\Delta AICc$	$w_i^{\ddagger}$	Log likelihood
344	2	0.00	0.43	-6419.42
211	2	0.94	0.27	-6419.89
87	2	1.79	0.18	-6420.32
106	2	4.67	0.04	-6421.76
10	2	4.81	0.04	-6421.83
5	2	5.20	0.03	-6422.02
150	2	6.66	0.02	-6422.75
Null	1	38.00	0	-6439.42

Table E6. Scale optimization model set for least cost distance to bay intertidal (m) around piping plover adult used and random points.

Least Cost Distance to Bay				
Model	$K^{\dagger}$	$\Delta AICc$	$w_i^{\dagger}$	Log likelihood
211	2	0.00	0.36	-6418.91
344	2	0.04	0.36	-6418.93
150	2	2.15	0.12	-6419.98
106	2	3.18	0.07	-6420.50
87	2	3.48	0.06	-6420.65
10	2	7.04	0.01	-6422.42
5	2	7.31	0.01	-6422.56
Null	1	39.03	0	-6439.42

Table E7. Scale optimization model set for Euclidean distance to vegetation (m) around piping plover adult used and random points.

Euclidean Distance to Vegetation				
Model	$K^{\dagger}$	$\Delta AICc$	$w_i^{\dagger}$	Log likelihood
344	2	0.00	1	-6383.32
211	2	35.72	0	-6401.19
150	2	44.26	0	-6405.45
106	2	48.23	0	-6407.44
87	2	51.00	0	-6408.82
10	2	70.21	0	-6418.43

5	2	70.59	0	-6418.62
Null	1	110.20	0	-6439.40

Table E8. Scale optimization model set for Euclidean distance to development (m) around piping plover adult used and random points.

Euclidean Distance to Development				
Model	$K^\dagger$	$\Delta AICc$	$w_i^\ddagger$	Log likelihood
211	2	0.00	0.32	-6243.9
150	2	1.13	0.19	-6244.5
106	2	1.82	0.13	-6244.8
87	2	2.05	0.12	-6245
344	2	2.27	0.1	-6245.1
10	2	3.05	0.07	-6245.5
5	2	3.13	0.07	-6245.5
Null	1	388.98	0	-6439.4

Table E9. Scale optimization model set for elevation (m) around piping plover adult used and random points.

Elevation				
Model	$K^\dagger$	$\Delta AICc$	$w_i^\ddagger$	Log likelihood
150	2	0.00	0.93	-6148.30
106	2	5.23	0.07	-6150.92

211	2	34.00	0	-6165.30
87	2	38.64	0	-6167.62
344	2	139.75	0	-6218.18
10	2	195.51	0	-6246.06
5	2	211.65	0	-6254.13
Null	1	580.24	0	-6439.42

Table E10. Scale optimization model set for slope (°) around adult piping plover used and random points.

Slope				
Model	$K^{\dagger}$	$\Delta AICc$	$w_i^{\dagger}$	Log likelihood
10	2	0.00	1	-5620.28
5	2	101.99	0	-5671.27
87	2	222.40	0	-5731.48
106	2	258.64	0	-5749.59
150	2	361.99	0	-5801.27
211	2	466.32	0	-5853.44
344	2	631.75	0	-5936.15
Null	1	766.52	0	-6004.53

CHAPTER 4. LINKING PIPING PLOVER CHICK ECOLOGY TO POST-HURRICANE LANDSCAPE

FEATURES

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Linking piping plover chick ecology to post-hurricane landscape features

RH: Robinson et al. • Piping plover chick ecology

Samantha G. Robinson¹, *Department of Fish and Wildlife Conservation, Virginia Tech, Blacksburg, VA 24061, USA*

Katie M. Walker, *Department of Fish and Wildlife Conservation, Virginia Tech, Blacksburg, VA 24061, USA*

Henrietta A. Bellman², *Department of Fish and Wildlife Conservation, Virginia Tech, Blacksburg, VA 24061, USA*

Daniel Gibson, *Department of Fish and Wildlife Conservation, Virginia Tech, Blacksburg, VA 24061, USA*

Audrey DeRose-Wilson⁴, *Department of Fish and Wildlife Conservation, Virginia Tech, Blacksburg, VA 24061, USA*

Daniel H. Catlin, *Department of Fish and Wildlife Conservation, Virginia Tech, Blacksburg, VA 24061, USA*

Sarah M. Karpanty, *Department of Fish and Wildlife Conservation, Virginia Tech, Blacksburg, VA 24061, USA*

Shannon J. Ritter, *Department of Fish and Wildlife Conservation, Virginia Tech, Blacksburg, VA 24061, USA*

James D. Fraser, *Department of Fish and Wildlife Conservation, Virginia Tech, Blacksburg, VA 24061, USA*

¹ Email: samgr@vt.edu

² Current affiliation: Delaware Division of Fish & Wildlife, 6180 Hay Point Lansing Rd, Smyrna, DE, USA 19977

³ Current affiliation: Florida Fish and Wildlife Conservation Commission, 1239 SW 10th St., Ocala, FL, USA 34471

Abstract

Population declines of disturbance-dependent species due to suppression of natural disturbances are realized across ecosystems. The piping plover (*Charadrius melodus*; plover), a disturbance-dependent and conservation-reliant shorebird that nests on sandy beaches and barrier islands on the Atlantic was listed under the United States Endangered Species Act in 1986. In 2012, Hurricane Sandy made landfall on Fire Island and Westhampton Island, barrier island nesting sites for plovers. Hurricane Sandy acted as a natural disturbance in this system, creating abundant nesting habitat. Chicks are a measure of reproductive output, and a better understanding of how chicks responded to Hurricane Sandy may improve plover habitat management and potentially species persistence. We evaluated the effects of post-Hurricane Sandy landscape features on resource selection, behavior, and survival of plover broods using logistic regression, generalized linear mixed effects models, and young survival models. Plover broods selected for flatter sites with less vegetation, and selected for sites farther from development as time since Hurricane Sandy increased. Chick foraging rates were highest in moist substrates and were negatively correlated with nesting plover density. Chick survival also was negatively correlated with nesting plover density, and survival was greater for earlier hatched broods. Further, chick survival was higher following an outbreak of sarcoptic mange in the local red fox (*Vulpes vulpes*) population, which substantially reduced the local fox

population. Generally, providing access to sites with flatter, moist substrates will likely result in more brood rearing habitat on the landscape. Ultimately, vegetation removal and habitat management may be needed to reduce plover nesting density, which may improve plover chick survival. Moreover, allowing hurricanes such as Hurricane Sandy to alter the landscape naturally, or not altering hurricane-created features, will create these landscape features.

KEY WORDS barrier islands, behavior, *Charadrius melodus*, chick survival, Hurricane Sandy, resource selection

Change in landscape characteristics, particularly habitat loss, is one of the most influential contributors to population change in wildlife taxa (Bonnot et al. 2017, Bar-Massada et al. 2019). Landscape characteristics are spatially and temporally dynamic, and their effects likely vary among species-specific life-stages (Miguet et al. 2016). To maximize species persistence probability on the landscape, a thorough understanding of landscape effects at all life stages is needed (Norris and Marra 2007). This need is particularly true for conservation reliant species, as conservation funding is limited and thus must be targeted efficiently.

Most early successional, or disturbance dependent species live in landscapes that are highly dynamic in space and time (Hunter et al. 2001), and these disturbance dependent habitats occur in nearly every ecosystem, including forests, prairies, and marine systems. Many species that rely on these habitats are in decline or have become extinct, in part due to human suppression of disturbance (Hunter et al. 2001). Barrier islands, highly dynamic, narrow, low-lying, strips of sand that lie adjacent to the mainland in some coastal systems (Leatherman 1988), are continuously transformed by storm and wave systems. Within a year, islands change as vegetation grows rapidly and storm related annual variations result in geomorphic changes to the

landscape (Maslo et al. 2019a). Species that occupy newly disturbed sites on barrier islands may then change their location between years or adapt to less-ideal conditions as the landscape matures (Maslo et al. 2019a). Thus, to manage a landscape following a disturbance that may benefit species, it is important to understand how species interact with and use habitat and at what point in succession habitat becomes unsuitable for disturbance-dependent species.

Piping plovers (*Charadrius melodus*; hereafter plover), temperate breeding shorebirds that occur on barrier islands in parts of their range, experienced range-wide population declines prior to their listing on the United States Endangered Species Act in 1986 (USFWS 1985). For the Atlantic Coast population, declines were primarily attributed to habitat loss, human disturbance, and predation (USFWS 1996). While all of these primary limiting factors have been addressed, continuous active management always may be required for this conservation reliant species (Scott et al. 2010, Goble et al. 2012). To reduce reliance on conservation measures, it will be most effective to determine management actions that would deliver long-term enhancements to population recovery, such as through widespread habitat creation or improvement measures (Goble et al. 2012). For Atlantic Coast plovers, hurricanes naturally act as habitat creation sources, allowing populations to rapidly increase for years following habitat creation events (Wilcox 1959, Cohen et al. 2009, Robinson et al. 2019).

In the fall of 2012, Hurricane Sandy struck the northeast United States, causing widespread damage to homes and landscape-level changes to ecosystems (Smallegan et al. 2016). The barrier island chains south of Long Island, which are nesting locations for plovers, were heavily altered (Walker et al. 2019, Zeigler et al. 2019). Hurricane Sandy thus created a system where plover response to disturbance and landscape change could be evaluated (Walker et al. 2019).

Landscape effects on plover nest site selection and survival to hatch have been evaluated but there is limited spatially explicit study of other life stages (i.e., adults, chicks; Maslo et al. 2016, Zeigler et al. 2017, Walker et al. 2019). Adult survival likely is driven by flyway-wide conditions, thus, it may be challenging to address locally (Norris 2005, Gratto-Trevor et al. 2012, Gibson et al. 2018, 2019, Weithman et al. 2018). The effect of landscape change on chick behavior and survival, alternatively, primarily are driven by local characteristics and therefore are more manageable on the breeding grounds. There are very few spatially explicit studies of the chick-rearing period, an essential component of reproductive output and population growth (USFWS 1985).

Population change in plovers is correlated with reproductive output (Saunders et al. 2018, Chapter 2). For Atlantic piping plovers, nest survival already is high where predator exclosures are used (Melvin et al. 1992). However, once the precocial chicks have hatched and begin to forage for themselves, the nest exclosure no longer protects them. Plover chick survival could be influenced by habitat suitability and would be reduced if chicks do not have access to adequate foraging habitat (Elias et al. 2000, Catlin et al. 2014, Walker et al. 2019). Thus, understanding resource selection and behavior of broods could help managers increase survival of piping plover chicks.

Habitat features likely are related to the effects of density, predation, and disturbance on plover chicks. Declines in habitat can result in elevated nesting density, lower carrying capacity, and increased intra- and interspecific aggression for density-dependent species (Royama 1977, Cubaynes et al. 2014, Goyert et al. 2017). Declines in habitat can reduce the effectiveness of camouflage and increase detection by predators, which also may interact with density if predators develop an improved search image of local prey. Increased human disturbance may

isolate and reduce available suitable habitat if it is made unavailable or unsuitable by temporal human disturbance or by direct effects on habitat (Walker et al. 2019).

Understanding the effect of landscape features on survival can determine whether habitat may be limited or acting as an ecological trap (Hale and Swearer 2016). Plover chick foraging behavior can influence their growth, resulting in differences in survival (Catlin et al. 2014). Reproductive output of plovers in the northeast has been assessed in terms of human disturbance (DeRose-Wilson et al. 2018) and relative to a more southerly site (Weithman et al. 2019). In addition, chick survival in plovers is negatively density-dependent (Hunt et al. 2018). Therefore, the next step in understanding variation in chick survival is to understand how habitat is interacting with density and other landscape features.

Plover behavior has frequently been studied, but habitat has primarily been assessed at a categorical level. Behavior is related to human disturbance (Burger 1994, DeRose-Wilson et al. 2018), and habitat (Loefering and Fraser 1995, Goldin and Regosin 1998, Elias et al. 2000, Le Fer et al. 2008b), with studies generally finding that plovers respond negatively to areas with frequent human disturbance and spend more time foraging in low wave energy moist habitats where invertebrates are abundant. However, like selection and survival, understanding of plover behavior may benefit from a finer-scale, spatially explicit analysis.

If it is determined that a specific landscape feature can positively influence reproductive output of plovers, future habitat management can attempt to replicate those features. To improve the understanding of the effects of fine-scale, spatially explicit landscape features on piping plover chicks, our objectives were to understand 1) plover chick habitat selection and 2) the influence of landscape features on plover chick survival and behavior. Plover broods and the adults tending them likely are selecting habitat to maximize survival and foraging opportunities

(Orians and Wittenberger 1991, Fraser and Catlin 2019). We hypothesized that chick survival would be lower in areas of more vegetation which can be used as concealment for terrestrial predators, and closer to development, which may attract plover predators and increase human disturbance. We hypothesized that plovers would select areas near higher invertebrate abundance for foraging, such as intertidal habitats, particularly low-wave energy moist habitats like bayside and ephemeral pools (Elias et al. 2000, Le Fer et al. 2008a). Further, we hypothesized that habitat suitability would be negatively correlated with habitat declines, and that chick survival would be negatively correlated with nesting density due to intra- and interspecific competition for space.

Study Area

We studied plovers on a 27-km stretch of Fire and Westhampton islands, barrier islands south of Long Island, during April to August, 2013–2019 (Fig. 1). The study area consisted of Fire Island National Seashore, managed by the National Park Service, Smith Point and Cupsogue Beach County Parks, managed by Suffolk County Parks, and Robert Moses State Park, managed by New York Parks, Recreation, and Historic Preservation.

These islands have the Atlantic Ocean to the south and several bays to the north (Fig. 1). Habitat types in the study area consisted of ocean-front sandy beaches, dunes, overwashes (areas where storm water carried sand landward over the island to the bay), bay-side sandy beaches, ephemeral pools, and breaches originally formed by Hurricane Sandy that were subsequently filled (Walker et al. 2019). The study area also included three inlets, Fire Island Inlet, Old Inlet, and Moriches Inlet. Old Inlet was formed by Hurricane Sandy and was left open, and Moriches and Fire Island inlets are dredged and stabilized with jetties to the east and west. Human use was

variable among the management areas with pedestrian and off-road vehicle use on various portions of the beach and boat access along the shoreline (DeRose-Wilson et al. 2018).

The plover population in the study area substantially increased from prior to Hurricane Sandy, in 2012, through the conclusion of this study in 2019 (Figure 2). Most of the population increase occurred after 2016, and nesting density increased with increasing population size (Fig. 3).

Plover chick predators in the study area include red fox (*Vulpes vulpes*), domestic cat (*Felis catus*), North American raccoon (*Procyon lotor*), common raven (*Corvus corax*), American Crow (*C. brachyrhynchos*), peregrine falcon (*Falco peregrinus*), merlin (*F. columbarius*), great black-backed gull (*Larus marinus*), herring gull (*L. argentatus*), and Atlantic ghost crab (*Ocypode quadrata*). Early in the study there were high densities of red fox in the study area, however mange outbreaks in 2015 and 2017, significantly reduced the local red fox densities (Robertson et al. 2019).

Methods

Field methods

Plover surveys occurred in subsites within the boundaries of management units and boundaries were based on local geomorphic qualities. We searched for plover nests by closely watching the ground and observing adult plover behavior. When a nest was found, we collected the location using a Garmin (Garmin International, Olathe, KS, USA) or Trimble GPS unit (Trimble Inc., Sunnyvale, CA, USA). If a nest was found with fewer than 4 eggs, we estimated initiation date assuming 1.5 days to lay each egg (Wilcox 1959, Haig and Oring 1988b). If a nest was found with 4 eggs, or after 4 days did not result in 4 eggs, we floated eggs to estimate initiation date

(Westerskov 1950). We monitored all nests every 1–3 days until they hatched or failed, and we considered nests that hatched ≥ 1 chick to be successful.

If eggs in a nest hatched, we banded all chicks as soon after hatch as possible (age range: 0–14 days) with either a combination of four-colored darvic plastic leg bands (2013), or a uniquely identifiable etched darvic plastic flag with a color band on the opposite leg (2014–2019). We conducted brood surveys every 1–3 days until chicks reached 30 days old by searching for banded chicks and associated adults in suitable habitat. Upon observation, we collected brood locations by first collecting an observer's location using a Trimble GPS unit (Trimble Geospatial, Sunnyvale, CA, USA), and offsetting that location with an azimuth from a compass and a distance from a Nikon 8397 Aculon Laser Rangefinder (Nikon, Minato, Tokyo, Japan; Robinson et al. 2020). We considered a plover chick fledged at 25 days post-hatch for consistency with past plover studies (Hunt et al. 2013, Catlin et al. 2015).

We conducted behavioral observations of a randomly selected chick in a brood using spotting scopes (DeRose-Wilson et al. 2018). Observations occurred between 05:46 and 17:20. We recorded foraging behaviors (peck, pull, drink), and every ten seconds, we recorded instantaneous behavior (forage, sit, run, walk, chase, flee, preen, encounter, out of sight), and habitat type (dry sand, moist sand, dry vegetation, moist vegetation, or wrack). If a chick was out of sight for ≥ 1 consecutive minute, we concluded the behavioral observations. All capture, handling, and observation procedures were conducted under Institutional Animal Care and Use Committee protocols #14-003 and #16-244, U.S. Geological Survey Federal Bird Banding permit #21446, U.S. Fish and Wildlife Service Endangered Species permit #TE-697823, U.S. National Park Service Scientific Research and Collecting permits FIIS-2013-SCI-002, FIIS-2015-SCI-0011, FIIS-2016-SCI-0003, FIIS-2017-SCI-0004, FIIS-2018-SCI-0004, New York

State Department of Environmental Conservation Endangered Species permit #314, New York State Office of Parks, Recreation and Historic Preservation permits 15-0700, 16-0393, 17-0755, 18-0168, 19-0128, and permits for Research in Suffolk County Parklands.

Image classification and variable creation

Aerial imagery and LiDAR were collected February to April of each year (Axis Geospatial, Easton, MD, USA). We classified fine-scale (15-cm) imagery for each year into four classes, dry sand, wet sand, vegetation and water, using the maximum likelihood classification tool in ArcGIS 10.6 (ESRI Inc., Redlands, CA, U.S.A.). We manually interpreted and digitized all development in the study area (i.e., parking lots, jetties, boardwalks) and incorporated the development into the habitat classification for another landcover class. Along with other aerial imagery, we collected LiDAR data each year at 1-m resolution, from which we created a digital elevation model (DEM). As the timing of aerial imagery did not always correspond with low tide, we used the DEM to identify intertidal areas. The oceanfront intertidal range was 0–1.2 m in elevation, based on the Astronomical High Water at NOAA Moriches Inlet tidal station, and the bayside intertidal range was 0–44.50 cm, based on mean high water at the NOAA Smith Point Bridge tidal station (NOAA 2014). We reclassified each DEM to select pixels within both the oceanfront and bayside intertidal and subtidal range. These pixels were reclassified to represent intertidal wet sand and water, respectively. The refined layers from each of these methods were superimposed over the classification. We resampled the classification to 1-m² pixels prior to creation of variable layers.

Based on our hypotheses, we created several variable layers using the classified imagery. We created rasters representing two proportion variables, dry sand proportion and vegetation proportion. To do this, we created a binary raster 500-m beyond our study area, where a cell value of 1 represented all dry or vegetation pixels, and 0 represented all other pixels. From these

rasters, the proportion of dry sand or vegetation around each cell was derived. To understand selection for foraging habitat, we created layers for Euclidean distance to ocean, Euclidean distance to bay, least cost path distance to ocean, and least cost path distance to bay. Least cost distance represents the distance it would take a walking plover to access bay or intertidal foraging habitat, assuming that any 1-m cell classified vegetation or water was a barrier to movement (Walker et al. 2019).

We also created layers that we hypothesized would represent selection for habitat that reduced predation risk, Euclidean distance to development and Euclidean distance to vegetation. Development in our study area could represent areas that avian and mammalian species use to take advantage of anthropogenic waste for food, including roads, parking lots, buildings, and constructed jetties. Development also could represent human disturbance as human use of the beach is typically clustered around parking lots and jetties for fishing (DeRose-Wilson et al. 2018). Vegetation, particularly clumps $\geq 1\text{m}$, could offer cover for terrestrial predators. Euclidean distance rasters were created using the ‘Euclidean Distance’ tool, and the least cost distance rasters were created using the ‘Path Distance’ tool in ArcGIS. We used the DEM to create an elevation layer. High elevation areas may increase susceptibility to aerial predators, such as gulls (*Laridae spp.*) or falcons. Finally, using ‘Slope’ in ArcGIS 10.6, we derived a slope layer from our DEM, hypothesizing that less steep areas would be selected for due to potential higher invertebrate abundance.

Density

We estimated nesting plover nesting pair density at the management unit scale (Figure 3). Using our delineated subsites, extending from the ocean to the bay, we calculated the hectares of dry sand in each subsite. Using Region Group in ArcGIS, we calculated the size of each dry sand patch in our study area using an 8-cell neighbor rule. We then removed all patches of dry sand

less than 1-m² of contiguous dry sand, and we summed the pixels of dry sand to represent available plover nesting habitat. We assessed density using the total number of pairs that nested in the management unit.

Resource selection

To determine the potential scale at which plover broods selected habitat, we used brood movement data. Using the ‘geosphere’ package in R, we calculated the movement of broods between successive daily observations (time between observations approx. 1 day) and between observations within a day, during 2014–2019. If we first observed the brood outside of the nest bowl, we added a location at the nest site on hatch day. For daily observations, if we collected more than one brood location in a day, we selected the last location collected in a day (Weithman 2019). We scaled locations by the time between observations, removing observations where the time between observations was greater than 1 day. We also calculated the distance from each brood location to their nest, not including any locations where broods were at or within 5m of their nest to account for GPS error (Robinson et al. 2020). We calculated the mean and median standardized distance a brood moved in 24hrs, the mean and median distance a brood moved between locations within a day, and the mean and median distance a brood was observed from their nest. Without prior knowledge of potential selection scales for plover chicks, all distances were used as potential scales that broods may be selecting landscape characteristics and were used as radii to create circular buffers around used and random brood locations.

Prior to modeling, we removed nest locations and any locations of broods <5m from their nest within 2 days of hatch. We generated 5 times as many random points as used points, restricted to wet or dry sand (Cooper and Millspaugh 2011). We only assessed resource selection within classified wet and dry sand, as plover brood detection probability is unknown but likely

lower in vegetated habitats. For 2014, random points were constrained to the eastern portion of the study area, as plovers were not monitored at Robert Moses State Park until 2015.

We extracted values from each of our variable rasters for the brood and random locations within circular buffers, where the radius was determined by the movement analysis results, using the ‘extract’ function in the *raster* package in R (Hijmans 2016). For the minimum circular buffer sizes, we used 5m and 10m (average and maximum error around GPS locations using offset methods; Robinson et al. 2020). To evaluate the effect size of each variable, we scaled all continuous variables using the mean and standard deviation.

We used scale optimization to determine the most relevant scale plover chicks selected each landscape variable. We developed separate, univariate model sets for each landscape variable. Within a set, each model evaluated plover chick resource selection using one of the scales identified in the brood movement analysis as a predictor variable (Chambers et al. 2016, McGarigal et al. 2016). We ranked each model within a set by AICc, selecting the best-supported scale (lowest AICc). If there was not one clearly supported scale, we selected the smallest scale with ≤ 2 AICc because, being a small organism, plovers likely make choices at relatively fine scales (Miguet et al. 2016). To reduce spatial autocorrelation, we spatially rarified the data by removing locations within years, and type of point (used or random) within 5m of all other points in the same year and type combination using SDMtoolbox for ArcGIS 10.6 (Brown et al. 2017).

We evaluated second-order resource selection (Jones 1980) by comparing plover brood use points to random points distributed in dry and moist sand. We used fixed-effects logistic regression models and evaluated four models. All models included all continuous landscape variables at the top selected scale, one model included additive effects of year, one included interactive effects with year, and one did not include year. We compared the three models to a

null model, allowing for the possibility that no selection was occurring. We interpreted the mean effect of each variable and the overlap of 95% confidence intervals with 0 from the top model.

We considered a variable significant if the 95% confidence interval did not overlap 0.

Behavior

To evaluate the effects of landscape characteristics on plover chick behavior, we used behavioral observations for which we had corresponding location data and where chicks were between 3 and 25 days (Elias et al. 2000). We grouped instantaneous behaviors into four groups, foraging, disturbed (encounter, chase, flee, or crouch), undisturbed (run, walk, stand, sit, brood, or preen), and other (Weithman 2019). We grouped broods into categorical habitat based on the habitat that comprised the greatest proportion of the behavioral observation. For the total time of the observation, we removed all instances of when the brood was out of sight.

We evaluated chick foraging rates (foraging attempts per minute; pecks/minute) with linear mixed effects models. We assessed the effect of the habitat type that the majority of the behavior observation was in (dry sand, dry veg, moist sand, moist veg, and wrack), brood age, quadratic brood age (to account for a non-linear response relative to age), least cost distance to ocean and bay, distance to development and vegetation, slope, elevation, dry sand proportion and vegetation proportion on foraging rate. We also included weather variables: daily average wind, daily average temperature, and daily precipitation. For dry sand proportion and vegetation proportion, we used the same circular buffer size around behavioral observations as for the resource selection analysis, but all other variables were measured as averages within 5m of the brood location. We developed an *a priori* model set, with models testing for the effects of year, categorical habitat, continuous habitat, age, quadratic age, all habitat variables, a model that evaluated predator avoidance, a model that evaluated foraging predictors, and a global model with all variables, resulting in 10 models. We included a nested random effect of subsite and nest

ID in every model. We scaled all continuous variables using the mean and standard deviation, and we tested for correlation between all continuous variables, removing one variable in a pair if correlation between pairs was $\geq |0.6|$. We evaluated models based on AICc (Burnham and Anderson 2002). We interpreted the mean effect of each variable and the overlap of 95% confidence intervals with 0.

Survival

To estimate chick survival, we used a modified Dail-Madsen model, a Bayesian implementation of the young survival from marked adults' model, applied in jags (Lukacs et al. 2004, Kellner 2018). We modeled chick survival for each year from 2013 to 2019. We estimated daily survival over a 25-day period using 5-day chick detection intervals. To estimate interval-specific chick survival for the whole study area, we developed a model with fixed effects of year and occasion on the survival parameter and a fixed effect of occasion on the detection parameter. To estimate the annual probability of survival to fledge (25 days), we calculated the product of the five 5-day interval survival rates.

We developed two models to understand whether chick survival was affected by landscape features, weather, density, or time. We included a linear trend of time, hatch day, maximum temperature, average wind speed, least cost distance to ocean, least cost distance to bay, distance to development, and nesting plover density. Distance and least cost distance variables were calculated as average distance within 5-meters of chick use points, averaged over the 5-day interval prior to detection.

We developed a second model without Westhampton Island broods to evaluate the effects of the sarcoptic mange outbreak in the red fox population, because we did not have information about the predator community at this site. In this second model, we included a brood-specific categorical variable of pre- and during mange as compared to post mange, to control for the

effect of the decline in the fox population on either side of the island. Plover density and predator trap success were measured at a management-unit level.

Chick survival models were built and implemented in a Bayesian framework, using the ‘jagsUI’ package to call Jags version 4.3.0 in R 3.5.2 (Kellner 2018, R Core Team 2018). We used vague priors for all estimated parameters. We assessed model fit diagnostics by visually inspecting MCMC chains and assuring the convergence ($\hat{R} \leq 1.05$) was reached (Gelman and Rubin 1992). We present estimates using the mean of the posterior distributions and the 95% Bayesian credible intervals. Model code is available in Appendix F.

Results

During 2013–2019, we monitored 234 broods, 11 of which were from 2013 when behavioral observations and locations were not recorded. During 2014–2019, we recorded 2743 locations and 1542 behavioral observations of pre-fledge plover chicks.

Resource selection

Scales.—The average age of broods during observations was 10.9 days (SD = 7.8), and the mean interval between observations was 1.7 days (SD = 1.4, median = 1.2). From locations where we observed broods on subsequent days (N = 1047), mean daily movement was 132 m (SE = 5, median = 88). For locations where we observed subsequent observations of broods on the same day (N = 378), the average time between locations was 60 minutes (SE = 6, median = 16).

Broods moved on average 98 m (SE = 6, median = 58). Broods were observed on average 224m (SE = 7, median = 141) from their nest. Therefore, from movement results, we used all average and median movement distances, 58, 88, 98, 132, 141, and 224m as circle radii in to evaluate average landscape features around brood and random locations. To assess the minimum scale at

which selection of various habitat variables was occurring, we used 5 and 10m, the average and maximum GPS error observed for these data (Robinson et al. 2020).

The best supported scale for plover brood resource selection varied among predictor variables (Tables G1–G8). Several variables (least cost distance to ocean, distance to development, and distance to development) were best described at the 5m scale. Vegetation proportion, slope, and elevation were best supported at the 58m scale, and the proportion of dry sand around locations was best supported at the broadest scale, 224m.

Resource selection.—Slope and elevation, both of which were best supported at the 58-m scale, were correlated ($r = 0.61$). Because both slope and elevation may be important for describing piping plover habitat and could influence invertebrate abundance, we compared the two using AICc prior to removing one of them. Slope was better supported, and we retained mean slope (scale = 58m) of locations in the resource selection model (Table H1).

Our best supported model to evaluate resource selection of plover broods following Hurricane Sandy included an interaction between all continuous variables and year (Table 1). Avoidance of vegetation (scale = 58-m) had the greatest effect on chick habitat selection, particularly in 2014 and 2015 (Figure 4). Similar to vegetation proportion, plover chicks avoided areas close to vegetation in all years except 2014. Plover broods selected for areas with less slope (scale = 58-m) in all years, but the 95% confidence intervals overlapped 0 in 2014 and 2015 (Figure 5).

Plover broods avoided areas with more dry sand in 2015 (scale = 224-m), no selection was evident in 2014, and in 2017 and 2019, broods avoided areas with less dry sand. During 2016–2019, there was a trend of broods selecting for areas farther from development (Figure 4). Broods in 2015, 2018, and 2019 selected sites closer to the bay intertidal. The mean effect

suggested plovers selected habitat closer to the bay in 2016, whereas no selection occurred for bay sites in 2017 or 2014. Plover broods in 2015 selected areas farther from the ocean, although the mean effect indicated selection for areas closer to the ocean in 2016–2019 but confidence intervals overlapped zero.

Behavior

During 2014–2019, we recorded 1290 observations of chicks between the ages of 3- and 25-days post-hatch, for which we had corresponding location data. Plover chicks spent the most time foraging when in moist sand (23.1%). Chicks spent the most time disturbed in dry veg (1.43%), although overall, chicks spent little time disturbed (1.37% of observations; Table 2). Mean foraging rate (pecks/minute) was greatest in moist veg, followed by moist sand, and was lowest in dry sand (Table 3).

Variation in peck rates was best described by the habitat model, which included continuous and categorical habitat variables (Table 4). The global model was the next most supported model, but $\Delta AICc$ was 16.95, and the habitat model held all model weight. The habitat that broods spent most of the behavior observation in was more influential to foraging rate than the continuous landscape variables (Figure 6). Peck rates were greater in moist habitats and wrack relative to dry sand, and peck rates were greater at lower elevations, and declined with increasing nesting plover density (Figure 6).

Survival

Chick survival to fledge was variable among years, with the lowest survival rate in the first year of the study, 2013, and the highest rate in 2018 (Figure 7). Based on the full chick survival model (i.e., including Westhampton Island), broods that hatched earlier in the summer had a higher probability of surviving to fledge than chicks hatching later, and the probability of a brood surviving to fledge increased as chicks aged. Chicks farther from the bay and in areas of lower

slope during a 5-day detection window had higher survival. Chick survival also increased with increasing temperatures and was lower when nesting density was high (Figure 8). Detection probability was high, and it did not vary substantially by occasion.

To simplify the model without Westhampton Island broods (resulting $N = 195$) we removed time varying detection probability because it was not influential across the whole study area. Chick survival was greater during the period after the fox population crash (Figure 8). Without Westhampton Island broods, chick survival was not affected by least cost distance to the bay or temperature, and the nesting density effect size nesting density decreased, however dry sand proportion became important, suggesting that broods in areas of less dry sand had higher survival (Figure 8). The influence of other predictors remained the same.

Discussion

Resource Selection

Plover chicks selected landscape features at different scales. The spatial scale of the effect of landscape variables can vary by species-specific dispersal distance, density, organism size, among other factors (Miguet et al. 2016). Chicks likely perceive the landscape at relatively fine scales, but at least some of their decisions are dictated by their tending parent, which are more mobile and likely have a broader perspective of the landscape (Chapter 3). However, chicks selected for the proportion of dry sand at the broadest scale of investigation, likely because chicks need to remain inconspicuous to predators (Camp et al. 2012, Claassen et al. 2018, Fraser and Catlin 2019).

The most influential variable to plover chick selection was the proportion of vegetation (scale = 58m). Similarly, we saw a decrease in probability of use as distance to vegetation increased. For plover chicks, vegetation likely represents an area of high predation risk as

vegetation can conceal terrestrial predators (Camp et al. 2012). However, as time since Hurricane Sandy increased, avoidance of vegetated areas declined, which suggests that, when available, broods will select for areas with less vegetation but can exhibit plasticity as the proportion of vegetation on the landscape increases (Elias et al. 2000, Morelli 2012).

Chicks increasingly selected for sites farther from development as time since Hurricane Sandy increased and as population size increased. This may be due to plovers increasingly being attracted to the sites farthest from development, namely the overwash and inlet sites, due to higher invertebrate abundance and habitat quality (Walker et al. 2019). Furthermore, following the sarcoptic mange outbreak on the western portion of the study area in 2017, densities increased at tip of Robert Moses State Park, possibly due to reduced persecution from terrestrial predators.

That plover chicks generally selected for areas of lower slope, suggested that plover chicks selected sites of moist substrate and avoided dune slopes. In addition, as slope was correlated with elevation, these lower slope sites tended to be at lower elevations. Moist substrates on barrier islands have higher invertebrate abundances (Loefering and Fraser 1995, Elias et al. 2000, Cohen et al. 2009, DeRose-Wilson et al. 2018), and thus broods likely are cuing in on this essential resource for growth (Catlin et al. 2014).

Behavior

Plover chick foraging rates were best explained by the dominant habitat type during behavioral observations. Peck rates were greatest in moist habitats, which is similar to other studies (Loefering and Fraser 1995, Goldin and Regosin 1998, Elias et al. 2000). Moist substrates have higher invertebrate densities and thus allow plover chicks to maximize their foraging efficiency, improve their growth rates, and enhance their chance of survival (Cohen et al. 2009, Catlin et al. 2014, DeRose-Wilson et al. 2018).

Plover peck rates were lower in management units with high plover nesting density. Plovers are highly territorial, and thus lower peck rates may have been related to antagonistic interactions between other plovers and chicks (Cohen et al. 2009, Catlin et al. 2011), or other beach nesting birds (Hogan et al. 2018). However, the decline in peck rates also could be correlated with other effects of population increase, such as decreased access to moist substrates because of territorial exclusion from nesting near high quality foraging habitat. Furthermore, as nesting density in the study increased, pairs likely settled in less ideal habitats, potentially areas with no high-quality foraging habitat nearby, so the decline in peck rates may have been due to more chicks being in poorer habitats.

Generally, broods in this study were disturbed at low levels during behavioral observations and disturbance did not vary by dominant habitat. During a similar study at Cape Hatteras National Seashore, potential disturbance during behavioral observations were infrequent and did not affect movement rates (Weithman 2019). However, in Rhode Island, broods in mudflat habitat spent less time disturbed (Goldin and Regosin 1998), and in New Jersey, adult plover vigilance was related to the number of people on the beach, regardless of habitat (Burger 1994, Hunt et al. 2019). Foraging rate and the proportion of time spent in moist habitats were lower on days with typically higher disturbance in this study (DeRose-Wilson et al. 2018), but we did not continue this analysis through 2019. The amount of disturbance that plovers experience is site dependent due to site-specific access and protection by management. Concurrent analysis of the effects of habitat and disturbance on plover vital rates may further elucidate the ultimate drivers of plover chick behavior on Fire and Westhampton islands.

Survival

Chick survival was higher in the post-mange years. Red foxes are known predators of plover nests (Patterson et al. 2011, Cohen et al. 2009, Doherty and Heath 2011), but causes of chick

mortality are challenging to document. Although we did not document foxes killing plover chicks, the negative correlation between the red fox numbers and chick survival suggests that they were responsible for a significant portion of chick mortality. However, the decline in the red fox population did not explain all variation in chick survival, as plover nesting density, temperature, and habitat also were influential (Cohen et al. 2009).

Chick survival also was negatively correlated with plover-nesting density. Plovers are territorial and compete for space during both the nesting and the brooding period (Elliot-Smith and Haig 2004). Higher plover nesting density can lead to intra-specific aggression, but also can improve a predator's ability to develop a search image for abundant prey (Whitfield 2003, Hunt et al. 2018a). Possible predators on the island that may have developed a search image for shorebirds include raccoons, owls, falcons, and gulls. Moreover, an increase in density often leads to an increase in plover intraspecific fighting, which is obvious to human observers and may increase detection by predators and reduced anti-predator vigilance by plovers (Catlin 2009). During the field study, chick predation by herring gulls and peregrine falcons was observed, and adult mortality by aerial predators increased, which may have extended to chicks. However, chicks are smaller than adults making their carcasses difficult to detect and/or easier to swallow whole.

The change in the effect of nesting density on chick survival once the fox variable was added in the model suggests that there may be some interaction occurring between predation by foxes, and fox or nesting density. This result would be expected if predation were density dependent in plovers (Hunt et al. 2018). The effect of predator removal and exclusion has been documented in plovers and other similar taxa. For example, on the Missouri River, chick survival increased following owl trapping and the data suggested predation on chicks was density

dependent (Catlin et al. 2011). In an experimental landscape for northern lapwings (*Vanellus vanellus*), Rickenbach et al. (2011) found that chicks protected from ground predators had higher survival rates than unprotected chicks. These results illustrate the importance of long-term data sets to understand temporal trends in vital rates, and the importance of simultaneously comparing several potential drivers of demography.

Comparison among analyses

The link between habitat selection and demographic processes is increasingly being made (Aldridge and Boyce 2007, Casazza et al. 2011, Catlin et al. 2019). We observed stronger relationships in selection than we did in survival, which may indicate that broods are adequately selecting quality habitat to maximize survival. Alternatively, there are likely many aspects of plover chick ecology that contribute to demography, thus relationships from other aspects than habitat selection could have led to attenuated relationships in demography. Following Hurricane Sandy, there was an abundance of suitable habitat (Walker et al. 2019), and following 2015 and 2018, on the east and west sides of Old Inlet respectively, plover broods no longer contended with red fox predation. The influence of increased habitat and primarily predator loss was supported in the high chick survival rates we observed in the study, and plasticity in selection for vegetation. The predation pressure in this system is dynamic, and therefore, continued study to determine whether increased predation by other predators through mesopredator release (Prugh et al. 2009), or through increased predation pressure by aerial predators, is needed (Whitfield 2003).

That least cost distance to bay, which we hypothesized would be a positive effect for all plover chick variables, did not positively influence any potential chick metrics, and instead negatively influenced chick survival, suggests that there is high quality habitat located elsewhere in the study area. Plovers elsewhere in the range can flourish despite not having access to

bayside habitat (Boettcher et al. 2007, Robinson et al. 2019). In this study, natural overwash and restoration habitats were not all characterized by bayside habitat, yet these sites frequently had high reproductive output and high adult fidelity. Further, natural overwash and restoration sites had low human use (DeRose-Wilson et al. 2018), which suggests that human disturbance was more influential than habitat in some cases. In this study, the sites with bayside access were small compared to the rest of the study area, and thus territoriality limited the access of these sites for most pairs. When plover nesting densities were low early in the study, least cost distance to bay was influential in predicting nest site locations (Walker et al. 2019). However, prior to the storm, in 2010, birds did not have access to the bay, and thus made other decisions to optimize their fitness, and they persisted, albeit in lower numbers. Therefore, there may be an interaction between nesting density and distance to bayside foraging habitat, the value of being close to bayside habitat is more of a binary variable than a continuous one (i.e., at bayside or not), or the relationships between plover chicks and bayside access is more complex than we represented here.

Overall, of the variables we looked at, the primary drivers of reproductive output were nesting plover density, moist substrates, vegetation, and predators. However, human disturbance, which was not included in models, also had an effect on reproductive output in this population (DeRose-Wilson et al. 2018). Direct disturbance by humans and predators likely influences all of the factors that assessed here (DeRose-Wilson et al. 2018). That earlier hatching broods had a greater probability of survival supports the idea that if human disturbance is reduced during the nesting period (i.e., beach driving restrictions), perhaps plover adults may nest earlier and thus give broods a higher chance of survival (Walker et al. 2019).

The direct estimation of population parameters, such as reproductive output and its constituent elements, are essential to understanding change in breeding populations of threatened species (Purvis et al. 2000). Reproductive output in this population contributes to population growth (Chapter 2), therefore it is essential that we manage to maximize the reproductive output on Fire and Westhampton islands (Cohen et al. 2009). Understanding brood home range size and movement also can lend to the understanding of reproductive dynamics in this population, as home range size and movement can be linked to survival or growth in some species (Nichols and Kaiser 1999, Lengyel 2006). Furthermore, as we saw that density affected both peck rates and survival, it may be helpful to create a geographic indicator of nesting plover density to determine if it also affects plover chick selection.

Management Implications

Hurricane Sandy positively affected plovers in this population, decreasing nesting plover densities and creating additional access to bayside foraging sites for chicks. To improve body condition and survival through improved foraging, access to moist habitats with little vegetation around them is crucial for plover chicks. However, in the absence of storms, vegetation removal is needed to maintain access to moist habitats and the early-successional states that are preferred by plovers. Vegetation removal also will reduce overall concealment ability of mammalian predators in plover nesting areas. Management to keep the red fox population at post-mange levels will likely allow the local piping plover to fully capitalize on the post-Hurricane Sandy habitat gains until carrying capacity is reached, but probably will not be able to push the plover population above the food-based carrying capacity.

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Tables

Table 1. Model selection table determine whether differences in piping plover brood resource selection is best determined by interactions with year. Predictor variables vary in scale. Least cost distance to ocean, distance to development, and distance to vegetation were measured at the 5-m scale. Proportion of vegetation, slope, and least cost distance to bay were measured at the 58-m scale. Dry sand proportion was measured at the 244-m scale.

Model	K ^a	Δ AICc	w_i^b	logLik ^c
Year * Predictors	48	0.00	1	-3231.07
Year + Predictors	13	85.46	0	-3309.06
Predictors	8	114.91	0	-3328.80
Null	1	889.41	0	-3723.06

^aNumber of model parameters ^bModel weight ^c Log likelihood

Table 2. Proportion of time piping plover broods were observed in foraging, undisturbed, and disturbed in each habitat type during a 5-minute behavioral observation. Foraging meant a chick was observed pecking, probing or drinking, undisturbed was run, walk, stand, sit, brood, or preen, and disturbed was encounter, chase, flee, or crouch. Proportions are represented as mean with standard error in parentheses.

Habitat	Foraging	Undisturbed	Disturbed
Dry Sand	0.11 (0.0056)	0.76 (0.0086)	0.014 (0.0021)
Dry Veg	0.095 (0.0096)	0.68 (0.019)	0.014 (0.0054)
Moist Sand	0.23 (0.011)	0.67 (0.013)	0.014 (0.0037)
Moist Veg	0.19 (0.046)	0.56 (0.061)	0.0083 (0.0057)
Wrack	0.15 (0.0067)	0.75 (0.0095)	0.0131 (0.0024)
All Habitats	0.14 (0.0041)	0.73 (0.0057)	0.014 (0.0014)

Table 3. Mean foraging attempts (peck, probe, pull) per minute (pecks/minute) for the dominant habitat type during piping plover brood observations.

	N	Mean Foraging	Max Foraging
Majority habitat		Rate (pecks/minute); SE	Rate (pecks/minute)
Dry Sand	537	4.90 (0.23)	36.00
Dry Veg	155	5.29 (0.44)	26.40
Moist Sand	259	10.90 (0.47)	48.20
Moist Veg	16	12.40 (1.75)	28.20
Wrack	323	6.70 (0.26)	22.40

Table 4. Model selection table for models describing habitat, weather, age, density, and year effects on piping plover brood foraging rates (pecks per minute) on Fire and Westhampton Islands, 2014–2019. Continuous habitat included least cost distance to bay intertidal (lc dist bay), least cost distance to ocean intertidal (lc dist ocean), distance to vegetation, distance to development, slope, elevation, % sand, % veg, and nesting plover density. Categorical habitat was defined by the habitat most of the behavioral observation occurred in (dry sand, dry veg, moist sand, moist veg, wrack).

Model	K ^a	ΔAICc	w _i ^b	logLik ^c
Habitat (Continuous + Categorical)	16	0	1	-1422.1
Global	27	16.95	0	-1419.1
Foraging (LC Dist Bay + LC Dist Ocean + Elevation + Slope)	7	97.15	0	-1479.9
Continuous Habitat	12	116.46	0	-1484.4
Categorical Habitat	7	287.54	0	-1575.1
Age + Age ²	5	435.79	0	-1651.2
Predators (sand proportion + veg proportion + nesting density)	6	448.99	0	-1656.8
Age	4	470.4	0	-1669.5
Weather	6	484.07	0	-1674.3
Year	8	489.26	0	-1674.9

^aNumber of model parameters ^bModel weight ^c Log likelihood

Figures

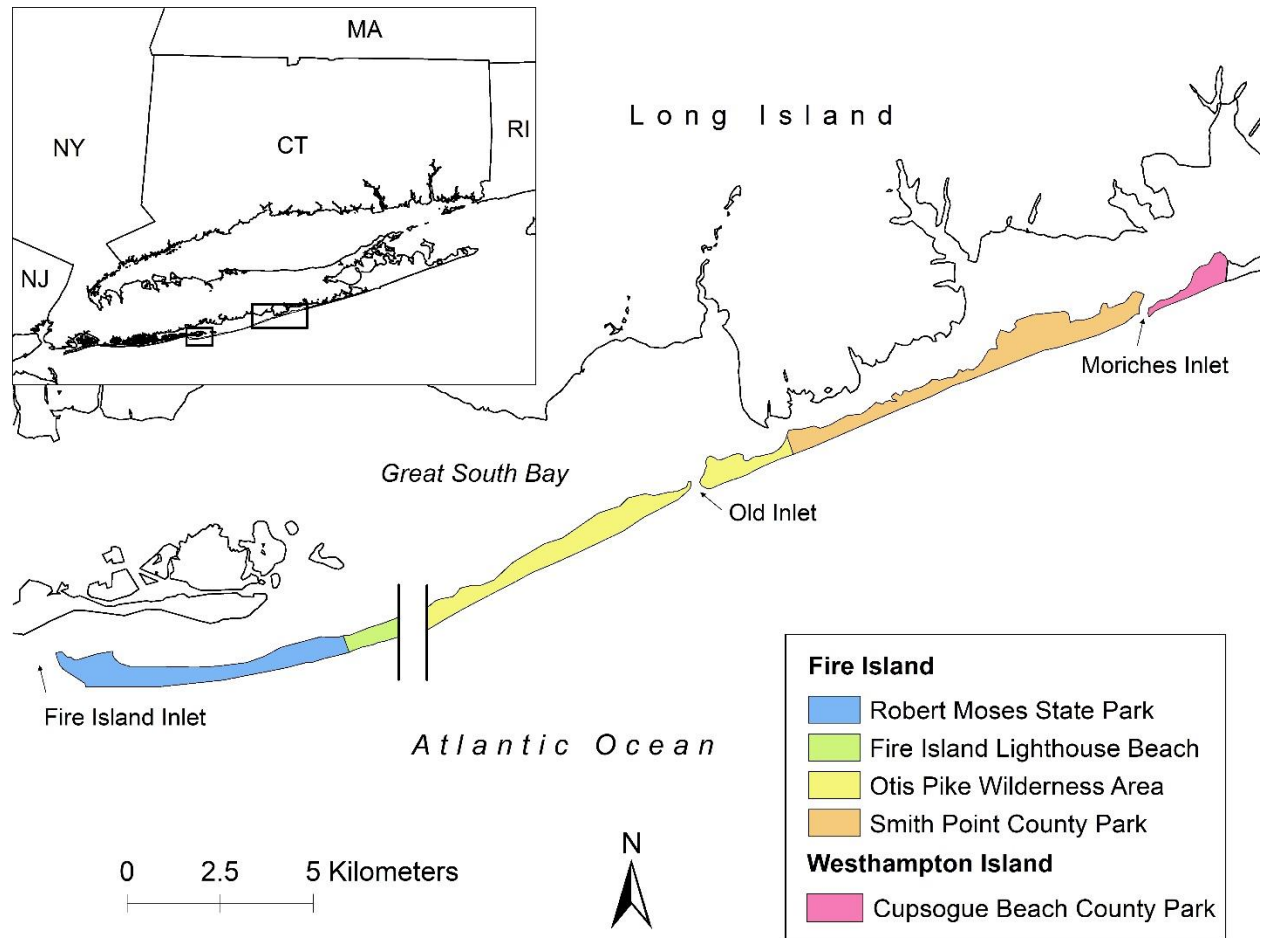


Figure 1. Study area where we monitored piping plovers during 2013–2019. Robert Moses State Park and the Fire Island Lighthouse Beach were added in 2015.

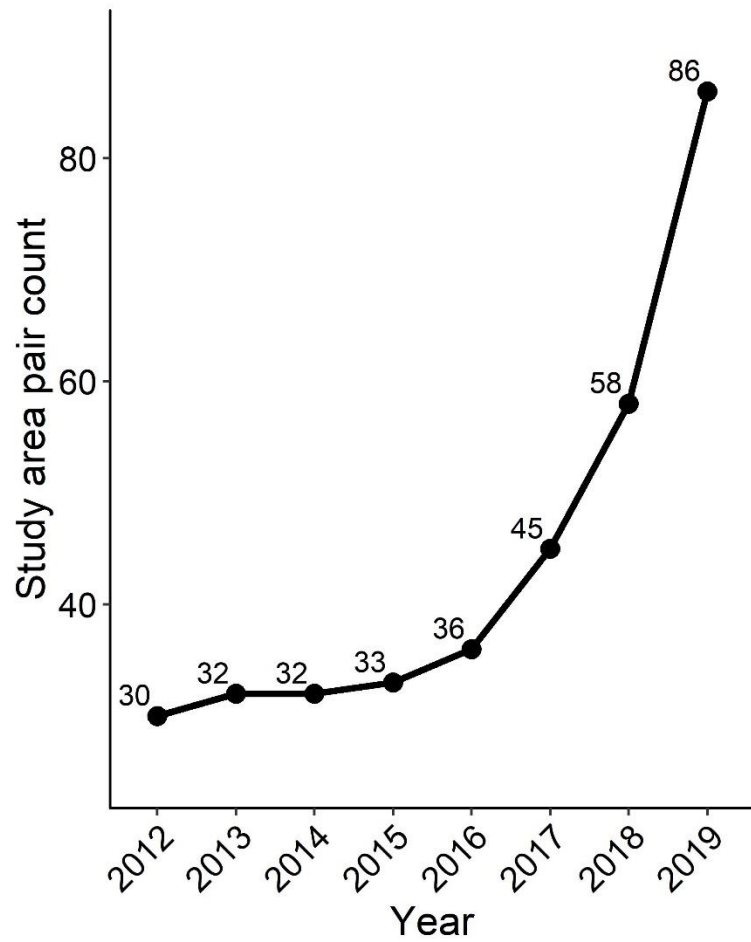


Figure 2. Estimated pair count within the study area from the year prior to Hurricane Sandy (2012) to the final year of the study (2019).

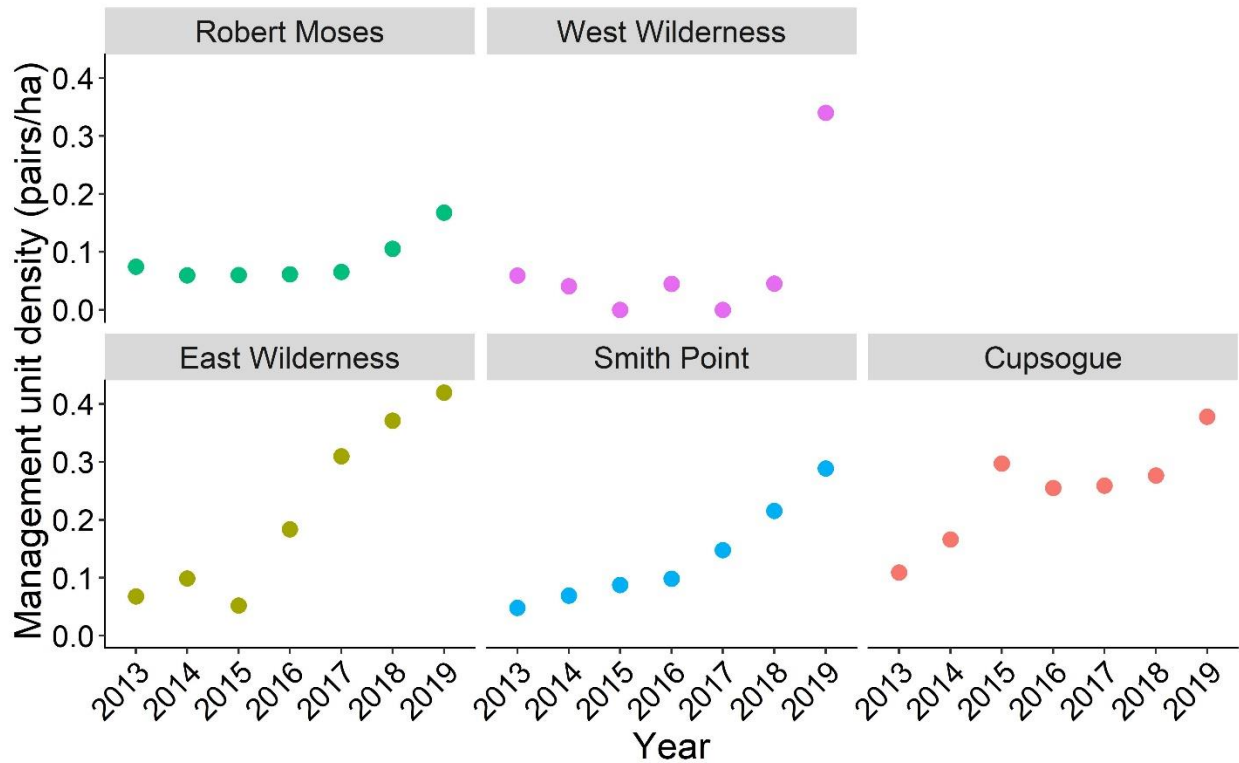


Figure 3. Estimated nesting plover density by management unit each year following Hurricane Sandy. Available habitat was defined as all available dry sand patches greater than 1m² using 15-cm classified aerial imagery. For 2013 and 2014, the number of pairs was a combination of the number of pairs monitored by Virginia Tech and the number of pairs estimated at Robert Moses State Park and the Lighthouse Tract. The Lighthouse Tract was grouped in with Robert Moses State Park for all years.

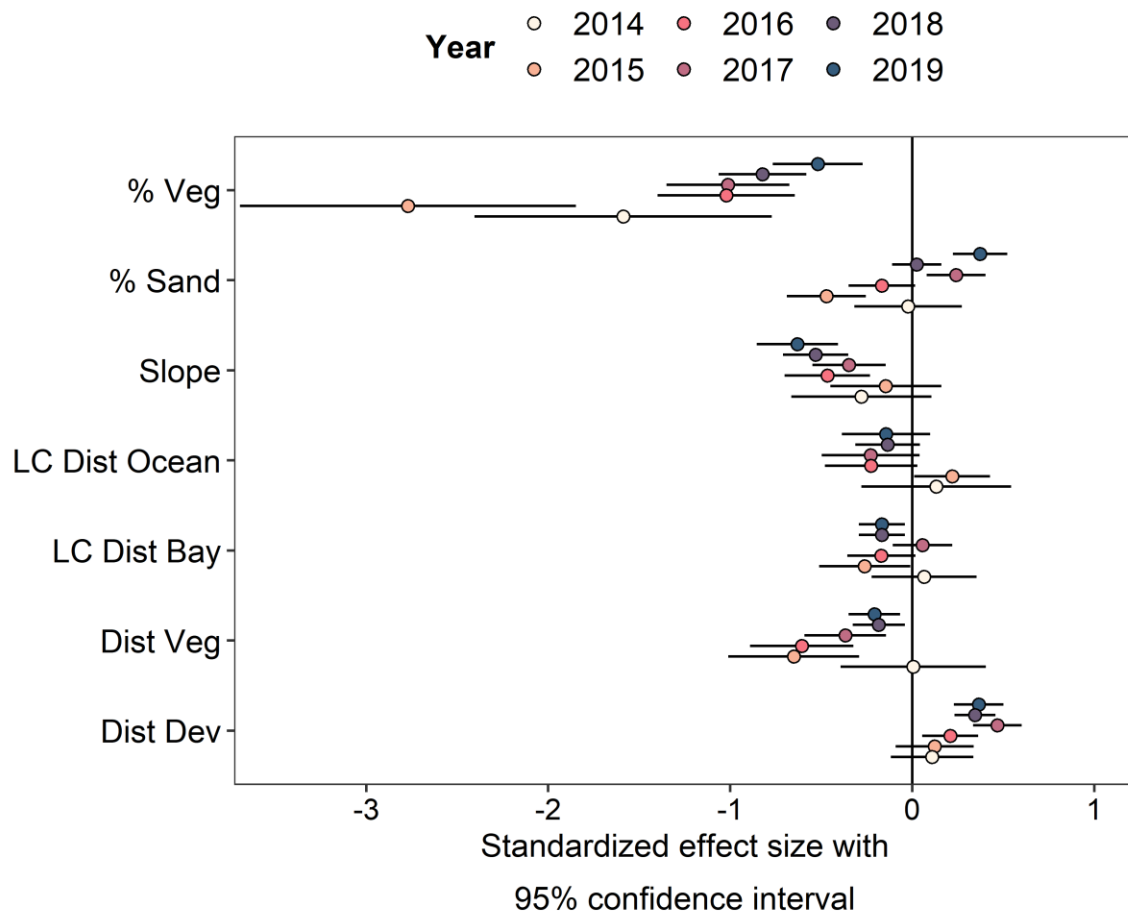


Figure 4. Standardized effect size for top ranked logistic regression resource selection function describing piping plover brood habitat selection on Fire Island, New York. For distance variable, a negative effect suggests selection closer to the feature and for proportion variables, a positive effect suggests selection with more of the feature within the specified buffer. Least cost distance to ocean, distance to development, and distance to vegetation were measured at the 5-m scale. Proportion of vegetation, slope, and least cost distance to bay were measured at the 58-m scale. Dry sand proportion was measured at the 244-m scale.

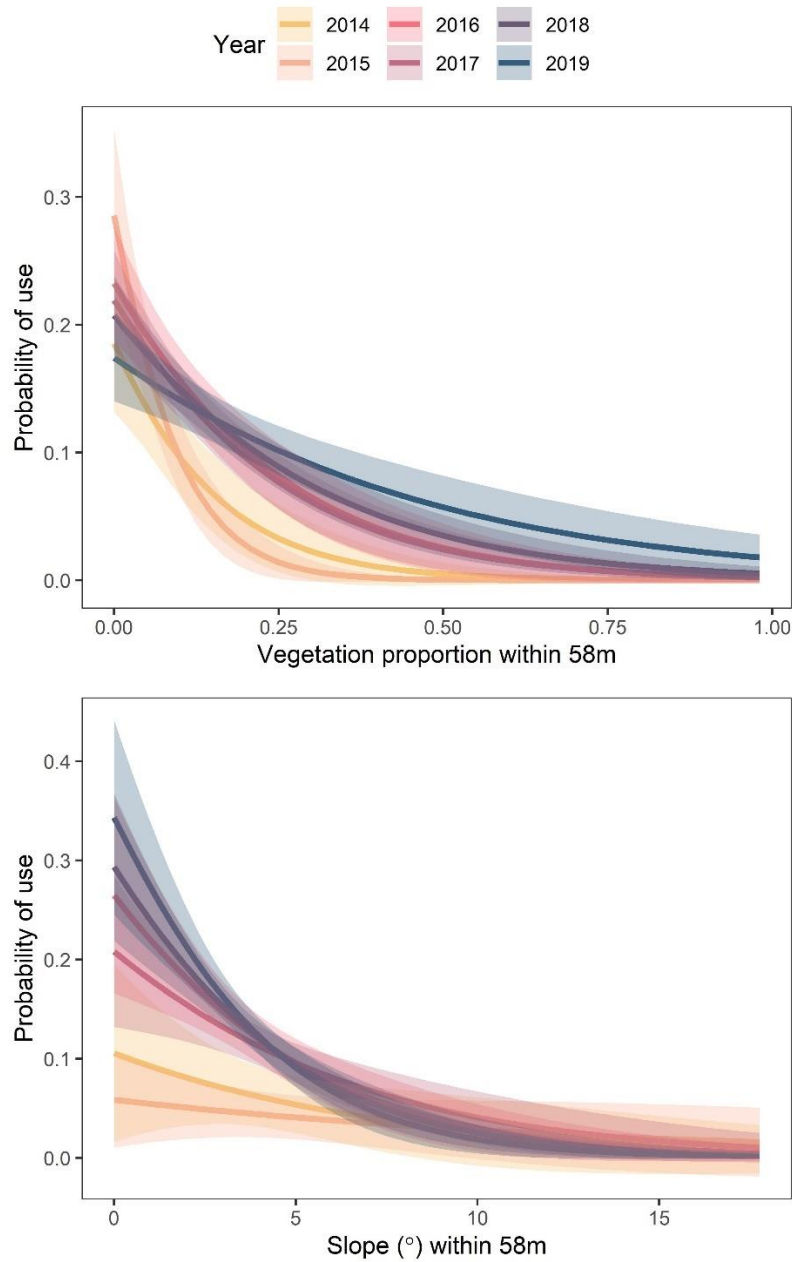


Figure 5. Predicted selection relationships for the top predictors of chick resource selection on Fire and Westhampton islands, 2014–2019. Predictions are derived from a logistic regression model with the interaction between year and all landcover variables. Each variable was measured at a different scale, as best described plover chick habitat selection via scale optimization.

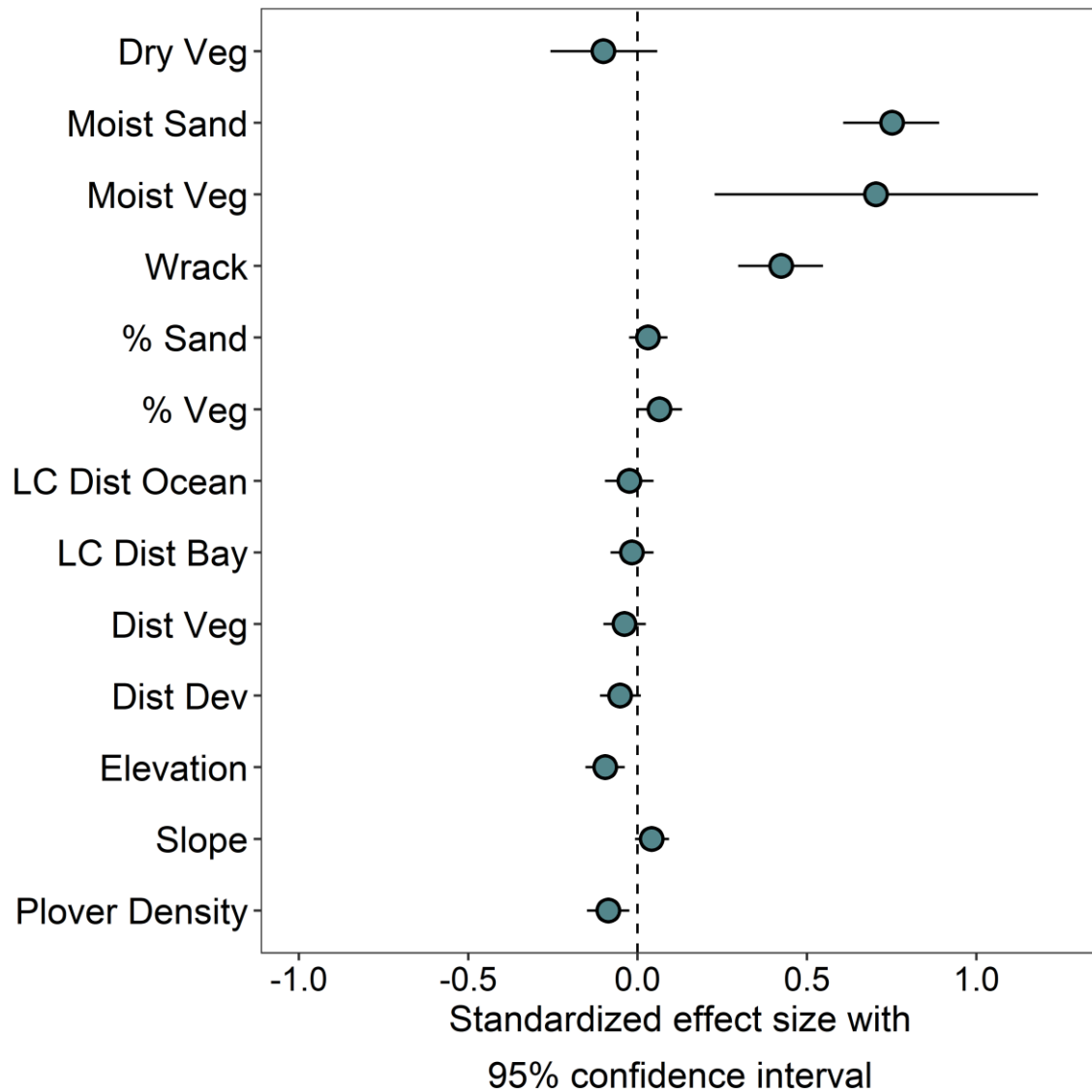


Figure 6. Standardized beta coefficients describing the relationships between peck rates (pecks/minutes) and categorical habitat and continuous habitat variables. Dry sand was the reference category. Model estimates are from a linear mixed effects model. Significance is interpreted as no overlap between 95% confidence intervals and 0, represented by the dashed vertical line.

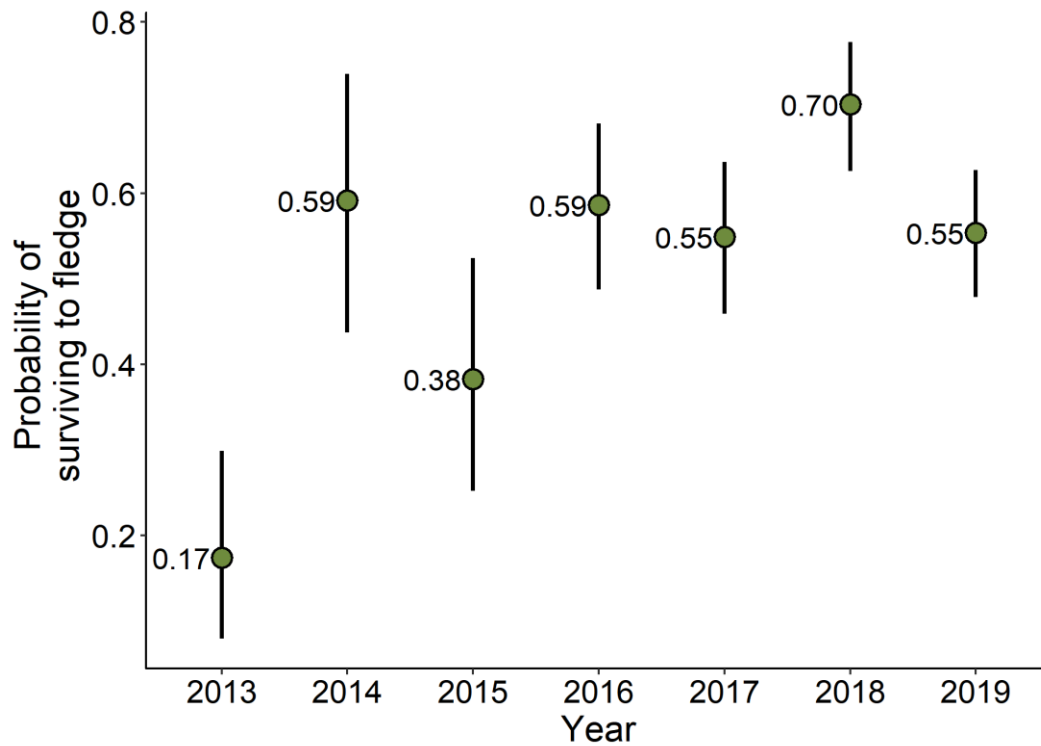


Figure 7. Probability of surviving to fledge (25 days) for chicks 2013–2019 on Fire Island and Cupsogue. Estimates are derived from a Dail-Madsen model modified for chick survival, and are the product of the 5-day interval specific probability of survival. Error bars represent 95% credible intervals.

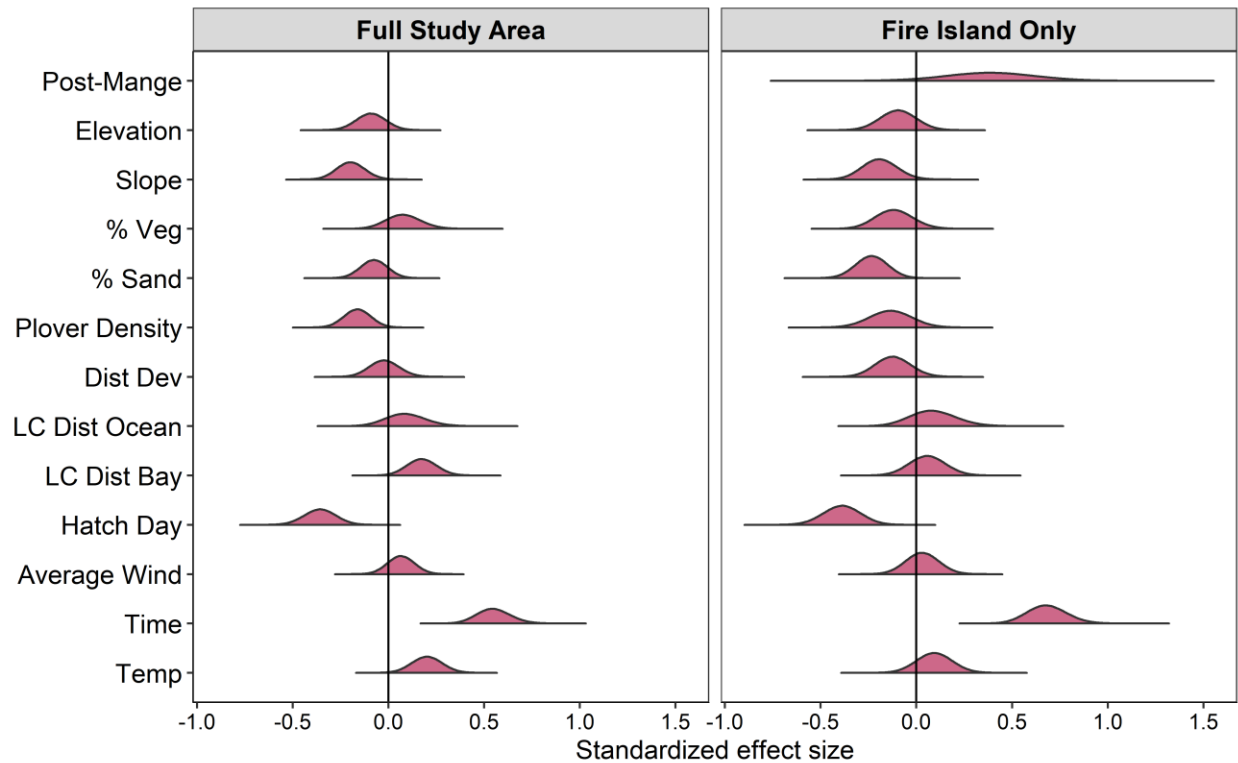


Figure 8. Distributions of standardized model coefficients from a chick survival model with the full study area (i.e., Fire Island and Westhampton Islands; left) and Fire Island only but including the effect on chick survival of pre- and during the sarcoptic mange outbreak on the red fox population, as compared to post-mange (right). Model estimates are from a modified Dail-Madsen model implemented in a Bayesian framework.

Appendix F. Supplementary model code for chick survival model implemented in JAGS

```
# Young Survival Model adapted from a Dail-Madsen Model (Dail and Madsen 2011),  
estimating the effects of habitat and weather on Fire Island and Westhampton Island  
piping plover chick survival, 2013–2019.
```

```
#Required packages  
library(jagsUI) #load the jagsUI library
```

```
#Original model developed by Gibson and Robinson for Robinson et al, (in review).
```

```
#Data definitions
```

```
n.years #number of years in the study  
n.broods #number of broods  
n.occasions #number of encounter occasions (5)  
y #brood by occasion capture history  
year.id.c #brood specific year vector  
occasion.v #vector of number of occasions c(1,2,3,4,5)  
temp #brood x occasion temperature matrix  
prcp #brood x occasion precipitation matrix  
wind #brood x occasion wind matrix  
density #brood specific density vector  
jdate #brood specific hatch date vector  
lcbay #brood x occasion least cost distance to bay matrix  
lcoit #brood x occasion least cost distance to ocean matrix  
distdev #brood x occasion distance to development matrix  
vprop #brood x occasion specific vegetation proportion matrix  
sprop #brood x occasion dry sand proportion matrix  
elev #brood x occasion elevation matrix  
slope #brood x occasion slope matrix
```

```
sink(file="bs_dm_vsprop_elev.jags")
```

```
cat("  
  model {
```

```
#####  
####
```

```
  # Model Priors
```

```
#####  
####
```

```
#####  
#####
```

```
mean.phic ~ dunif(0,1)  
mean.pc ~ dunif(0,1)
```

```

mu.phic <- log(mean.phic/(1-mean.phic))
mu.pc <- log(mean.pc/(1-mean.pc))

mixing ~ dbeta(2.5, 25) # Constant brood immigration parameter, brood emigration is
constrained with phi

#Priors for model parameters
beta.time.c ~ dnorm(0,0.001)
beta.time.pc ~ dnorm(0,0.001)
beta.temp.c ~ dnorm(0,0.001)
beta.wind.c ~ dnorm(0,0.001)
beta.jdate.c ~ dnorm(0,0.001)
beta.lcbay.c ~ dnorm(0,0.001)
beta.lcoit.c ~ dnorm(0,0.001)
beta.distdev.c ~ dnorm(0,0.001)
beta.density.c ~ dnorm(0,0.001)
beta.vprop.c ~ dnorm(0,0.001)
beta.sprop.c ~ dnorm(0,0.001)
beta.slope.c ~ dnorm(0,0.001)
beta.elev.c ~ dnorm(0,0.001)

for(j in 1:n.broods) {
  for (t in 1:(n.occasions - 1)){
    logit(phi[j,t]) <- mu.phic + beta.time.c*occasion.v[t] + beta.density.c*density[j] +
beta.wind.c*wind[j,t] + beta.temp.c*temp[j,t] +
    beta.jdate.c*jdate[j] + beta.lcbay.c*lcbay[j,t] + beta.lcoit.c*lcoit[j,t] +
beta.distdev.c*distdev[j,t] + beta.vprop.c*vprop[j,t] + beta.sprop.c*sprop[j,t] +
beta.slope.c*slope[j,t] + beta.elev.c*elev[j,t]
  }
}

for (t in 1:(n.occasions - 1)){
  logit(count.p[t]) <- mu.pc + beta.time.pc*occasion.v[t]
}

#####
# Model
#####
# Assign constraints on initial brood size
for(j in 1:n.broods) {

N[j,1] <- y[j,1] # Model assumes perfect detection of initial brood sizes

```

```
#####
#
# S: Number of individuals that survived (latent state)
# G: Number of individuals that immigrated into brood (latent state)
# N: Number of individuals associated with a brood (latent state)
# y: encounter history

#####
#
  for(t in 2:n.occasions) {
    S[j,t-1] ~ dbin(phi[j, t-1], N[j,t-1])
    G[j,t-1] ~ dpois(mixing * N[j,t-1] * phi[j,t-1])
    N[j,t] <- S[j,t-1] + G[j,t-1]
    y[j,t] ~ dbin(count.p[t-1], N[j,t])
  }
  # for (k in 1:n.years){
  #   for(t in 1:n.occasions) {
  #     Nt[k,j,t] <- ifelse(year.id.c[j] == k, N[j,t], 0)
  #   }
  # }
}

}

", fill=TRUE)
sink()

# Bundle Data
dat <- list(n.broods=n.broods, n.occasions=n.occasions, y=y, year.id.c=year.id, n.years
= n.year, occasion.v = occasion.v, temp = tempcompress_s, prcp = prcpcompress_s,
wind = windcompress_s, density = as.numeric(maxchickcompress$density), jdate =
as.numeric(maxchickcompress$jdate, lcbay = lcbay.cs, lcoit = lcoit.cs, distdev =
distdev.cs, distveg = distveg.cs, fox.id.c = fox.id.c, vprop = vprop.cs, sprop = sprop.cs,
elev = elev.cs, slope = slope.cs)

# Initial values
Ni <- y + 10
Si <- Ni[,2:n.occasions]
Si[] <- 1
Gi <- Ni[,-1]-Si
Ni[,-1] <- NA

init<- function() list(S=Si, G=Gi)
```

```
pars <- c("mixing", "p", "annual.phi", "beta.temp.c", "beta.time.c", "beta.prcp.c",
"beta.wind.c",
      "beta.jdate.c", "beta.lcbay.c", "beta.lcoit.c", "beta.distdev.c", "beta.density.c",
      "beta.sprop.c", "beta.vprop.c", "beta.time.pc", "beta.slope.c", "beta.elev.c",
"count.p")
```

```
n.iter <- 750000
n.thin <- 2
n.burnin <- 150000
n.cores <- 3
n.adapt <- 150000
n.chains <- 3
```

```
#####
#####
# compile model
#####
#####
brood_survival_full <- jags(dat, init, pars, "bs_dm_vsprop_elev.jags", parallel = TRUE,
n.chains = n.chains, n.adapt = n.adapt, n.iter = n.iter, n.burnin = n.burnin, n.thin = n.thin,
n.cores = n.cores)
```

Appendix G. Scale optimization model sets

For all tables, ^aNumber of model parameters ^bModel weight.

Table G1. Scale optimization for dry sand proportion around piping plover brood used and random points.

Dry Sand Proportion				
Model	K ¹	ΔAICc	wi ²	Log likelihood
224	2	0.00	1	-4926.18
141	2	34.46	0	-4943.41
132	2	39.15	0	-4945.76
98	2	54.96	0	-4953.66
88	2	59.04	0	-4955.70
5	2	67.16	0	-4959.76
58	2	68.86	0	-4960.61
Null	1	73.21	0	-4963.79
10	2	73.99	0	-4963.18

Table G2. Scale optimization for vegetation proportion around piping plover brood used and random points.

Vegetation Proportion				
Model	K ¹	ΔAICc	wi ²	Log likelihood
58	2	0.00	1	-4659.57
88	2	38.20	0	-4678.67
98	2	50.08	0	-4684.61

10	2	80.64	0	-4699.89
132	2	99.59	0	-4709.37
141	2	112.82	0	-4715.98
224	2	171.95	0	-4745.55
5	2	176.80	0	-4747.98
Null	1	606.43	0	-4963.79

Table G3. Scale optimization for least cost distance to bay intertidal (m) around piping plover brood used and random points.

Least Cost Distance to Bay				
Model	K ¹	$\Delta AICc$	w_i^2	Log likelihood
224	2	0.00	0.28	-4959.59
141	2	1.16	0.15	-4960.17
132	2	1.53	0.13	-4960.35
98	2	1.59	0.12	-4960.38
88	2	1.82	0.11	-4960.50
58	2	1.84	0.11	-4960.50
10	2	3.65	0.04	-4961.41
5	2	4.00	0.04	-4961.58
Null	1	6.41	0.01	-4963.79

Table G4. Scale optimization for least cost distance to ocean (m) around piping plover brood used and random points.

Least Cost Distance to Ocean				
Model	K1	ΔAIC_c	wi_2	Log likelihood
10	2	0.00	0.57	-4936.08
5	2	0.93	0.36	-4936.54
58	2	4.11	0.07	-4938.13
88	2	11.86	0	-4942.01
98	2	14.29	0	-4943.22
141	2	24.22	0	-4948.19
132	2	24.41	0	-4948.28
224	2	27.05	0	-4949.60
Null	1	53.43	0	-4963.79

Table G5. Scale optimization for Euclidean distance to vegetation (m) around piping plover brood used and random points.

Distance to Vegetation				
Model	K1	ΔAIC_c	wi_2	Log likelihood
10	2	0.00	0.49	-4929.71
5	2	1.04	0.29	-4930.24
58	2	1.64	0.22	-4930.53

88	2	10.54	0	-4934.98
98	2	12.70	0	-4936.07
224	2	14.64	0	-4937.03
132	2	17.99	0	-4938.71
141	2	18.97	0	-4939.20
Null	1	66.15	0	-4963.79

Table G6. Scale optimization model set for Euclidean distance to development (m) around piping plover brood used and random points.

Distance to Development				
Model	K1	$\Delta AICc$	$wi2$	Log likelihood
5	2	0.00	0.23	-4843.94
10	2	0.17	0.21	-4844.03
58	2	0.68	0.17	-4844.28
88	2	1.47	0.11	-4844.68
98	2	1.69	0.1	-4844.79
132	2	2.39	0.07	-4845.14
141	2	2.57	0.06	-4845.23
224	2	3.58	0.04	-4845.73
Null	1	237.69	0	-4963.79

Table G7. Scale optimization model set for elevation (m) around piping plover brood used and random points.

Elevation				
Model	K1	$\Delta AICc$	wi^2	Log likelihood
58	2	0.00	1	-4786.38
10	2	22.02	0	-4797.39
88	2	34.86	0	-4803.81
5	2	35.30	0	-4804.03
98	2	46.25	0	-4809.51
132	2	86.21	0	-4829.49
141	2	95.49	0	-4834.13
224	2	158.73	0	-4865.75
Null	1	352.81	0	-4963.79

Table G8. Scale optimization model set for slope (°) around piping plover brood used and random points.

Slope				
Model	K^1	$\Delta AICc$	wi^2	logLik
58	2	0.00	1	-4700.20
10	2	90.66	0	-4745.53
88	2	96.38	0	-4748.38
98	2	123.94	0	-4762.16
5	2	139.71	0	-4770.05

132	2	208.39	0	-4804.39
141	2	228.24	0	-4814.31
224	2	361.23	0	-4880.81
Null	1	525.19	0	-4963.79

Appendix H. Correlated variable selection

Table H1. Model selection table determining whether slope or elevation better described variation in piping plover chick resource selection. The top variable was included in all resource selection models to evaluate piping plover brood habitat selection 2014–2019 on Fire and Westhampton Islands, NY.

Model	K ^a	ΔAICc	w _i ^b	logLik ^c
Slope	2	0.00	1	-3533.96
Elevation	2	122.40	0	-3595.16

^aNumber of model parameters ^bModel weight ^c Log likelihood

CONCLUSION

Throughout their breeding range, piping plovers (*Charadrius melodus*; plover) are limited by available nesting habitat, supported by population increases following widespread habitat creation or improvement (Robinson et al. 2019). Although breeding plover populations consistently increased following habitat creation, demographic mechanisms of increase were less clear. The primary drivers of population change were likely increased immigration and reproductive output, as adult survival is a relatively stable rate in this species (Calvert et al. 2006, Cohen and Gratto-Trevor 2011, Catlin et al. 2015, Hunt et al. 2018, Weithman et al. 2019). However, the contribution of immigration or reproductive output to individual population increases was variable, likely due to localized habitat, predator abundance, and population connectivity conditions (Catlin et al. 2016, Zeigler et al. 2017).

On Fire Island, we investigated local population change with a long-term banding study and population monitoring data. Hurricane Sandy increased available nesting habitat at least 150% on Fire Island (Walker et al. 2019), and as predicted from past habitat creating events, the population increased at least 90% by 2018. For the Fire Island irruption, the primary driver of population increase was immigration. Immigration must also have been a significant contributor to population change in past population irruptions, where reproductive output was not always high following the event (Boettcher et al. 2007). Immigration likely also sustains other populations, such as the Outer Banks of North Carolina (Weithman et al. 2019), but in some cases, such as the Missouri River following flooding in 2011 where the increase in habitats was very substantial, reproductive output was high enough to be more influential than immigration (Hunt et al. 2018).

In addition to natural habitat creation, man-made habitat has been created for several shorebird and waterbird taxa (Powell and Collier 2000, Masero 2003, Davis et al. 2008, Maslo et al. 2012, Catlin et al. 2015). However, the success of created habitats should be assessed prior to widespread implementation, as they may improve outcomes, but not always on par with naturally created habitat (Hunt et al. 2018). On Fire Island, restoration areas created to mitigate potential habitat loss due to the Fire Island to Moriches Inlet Stabilization Project had higher chick survival, but on average, nest survival, and breeding fidelity were lower for these sites. Combined, the restoration areas had similar reproductive output and equal population growth to the rest of the study area and were generally improved habitat relative to what was in the footprint of the sites prior to creation (Walker et al. 2019, Chapter 3). Thus, the creation of the restoration areas contributed positively to population growth and they were on par with naturally created habitat. However, of two restoration sites, the largest (Great Gun; 34.8 ha) had a greater influence than the smaller (New Made; 6.6 ha) restoration area, likely due to combined influences of size, having slower revegetation rates, and having consistent access to oceanside foraging habitat and wrack.

Nesting and foraging habitat are needed for success of breeding shorebird populations (Atkinson 2003). Natural coastal dynamics make long-term creation of intertidal or ephemeral habitats challenging, and the colonization of invertebrate communities in restored habitats also is of concern in restored habitat. Piping plovers respond positively to creation of engineered habitats (Catlin et al. 2011a, McIntyre and Heath 2011, Catlin et al. 2015, Walker et al. 2019), and natural habitats (Hunt et al. 2018). However, adequate foraging habitat must be available adjacent to created nesting habitat. Thus, although engineered habitat creation was successful in this case, future habitat engineering projects should build off design criteria for the larger

restoration area, as the smaller restoration area lost access to foraging habitat due to vegetation encroachment and nesting ceased in 2017. Future restoration efforts also should improve access to low energy intertidal habitats or improve foraging pond construction where possible (Maslo et al. 2011, 2012).

As immigration was the most influential demographic parameter to the localized population growth on Fire Island, it was particularly important to understand how to improve habitat for adults on Fire Island and Westhampton Island. During the 5-month breeding season, adult plovers transition through different breeding stages and behaviors. We detected differences in habitat selection between parental and non-parental behaving adults, primarily in relation to dry sand, development, distance to bay intertidal, and elevation. Non-parental adults avoided dry sand, and did not select for bay intertidal habitat whereas parental adults selected for both features. Non-parental adults also selected for sites farther from development and at lower elevations relative to parental adults. Each year, there was more suitable habitat for parental plovers than non-parental plovers. Furthermore, the restoration areas mapped as highly suitable for parental plovers, and less suitable for non-parental plovers.

To increase carrying capacity of nesting plovers on Fire Island and Westhampton Island, habitat suitability for adult plovers aside from just nest locations should be considered, as adults may assess habitat for needs other than nesting alone. Given there was more suitable habitat for parental plovers than non-parental plovers, habitat management could strive to increase availability of habitats suitable for non-parental plovers. Habitats for needs other than breeding do not receive the same level of protection as breeding habitat, thus protection should be increased in the ocean intertidal habitats during pre- and post-breeding periods (Hevia and Bala 2018, Walker et al. 2019). Vegetation removal to reduce predation and lowering elevation and

slope to improve foraging efficiency also likely will increase suitable habitat amounts for all breeding and behavior stages on Fire Island (Whittingham et al. 2002, Swaisgood et al. 2018). Reproductive output was the second most influential parameter affecting population increase on Fire Island and Westhampton Island as indicated by moderate correlation between reproductive output and population growth. Therefore, local management also should prioritize high reproductive output. In this study, we specifically evaluated the chick rearing period, as nests in the study area typically were exclosed and thus much less vulnerable to loss were than chicks (Ivan and Murphy 2005, Maslo and Lockwood 2009, Barber et al. 2010). Several variables were influential to improving habitat, foraging, and survival of plover chicks. Plover chicks selected for sand with less vegetation and sites with less slope as compared to random locations. Foraging rates were highest in moist substrates, at lower slopes, and in sites with lower plover nesting densities. Plover chick survival was higher in flatter areas, sites with lower nesting plover densities, and following a substantial decline in the local red fox (*Vulpes vulpes*) population due to sarcoptic mange.

Habitat and predators influence plover chicks throughout the breeding range (Ivan and Murphy 2005, Catlin et al. 2011b, 2015, Hunt et al. 2018). Nesting density and habitat amount, as is to be expected in a highly territorial species, relate to variation in chick survival (Cohen et al. 2009, Hunt et al. 2018). Plover chicks in bay and interior habitats of Assateague Island National Seashore had higher survival than on the oceanfront beaches (Loefering and Fraser 1995). Access to high quality food resources is consistently supported as important for piping plover chicks (Catlin et al. 2014). However, predation also is influential when considered in conjunction with foraging resources (Le Fer et al. 2008, Catlin et al. 2011b).

There was a possible interaction between nesting density and chick predation, as evidenced by the change in the importance of nesting density on chick survival when predation was added into the model. Density-dependent predation is a well-known phenomenon (Page et al. 1983, Whitfield 2003, Hunt et al. 2018). Although we only evaluated the change in abundance of a single terrestrial predator on plover chick survival, other predators also certainly affected the local plover community. Mesopredator release following the loss of red fox is possible and has been observed in other nesting plover populations (Prugh et al. 2009, Beaulieu et al. 2014), although we have limited evidence mesopredator release in our system (K. Black, personal communication). We also documented a numerical increase in adult mortality from aerial predators following the red fox population crash, but more study is needed to determine if the increase resulted in lower average adult survival, as most mortality occurred in the final two years of the study. Increased mortality may be due to increased plover abundance, with peregrine falcons (*Falco peregrinus*) and owls developing a search image of piping plovers in areas with increased abundances. However, we did not monitor aerial predator populations and thus are unable to estimate changes in falcon or owl numbers.

Although not studied here, the effect of disturbance in conjunction with chick ecology needs further study, as chick survival and foraging rates are lower in higher human use sites (DeRose-Wilson et al. 2018). Earlier hatch dates improve survival (Catlin et al. 2014), which also was supported for Fire Island chicks. However, on Fire Island and Westhampton Island, some areas are fenced to exclude people prior to nesting, but much suitable nesting habitat is not protected (Walker et al. 2019). Reducing early-season disturbance in suitable habitats by protecting larger areas or restricting beach driving earlier in the season may allow earlier nesting and overall higher reproductive output. Human disturbance also can reduce the local prey

availability (Schlacher et al. 2016), possibly reducing chick survival by starvation or by increasing aggressive interactions. Thus, managing the functional reduction of available habitat due to human disturbance is essential alongside managing geomorphic and structural habitat. On both Fire Island and Westhampton island and in the restoration areas, the nesting population took >1 year post-habitat creation to rapidly increase. These rapid increases, while possible because of available nesting habitat, likely also were partially related to the decline of the local red fox population. Some of the increase also could have been due to conspecific attraction, such that prospecting individuals following the breeding season assessed the local conditions on Fire Island and found them favorable (Ahlering and Faaborg 2006, Davis et al. 2017). Indeed, in instances when we observed adults from Robert Moses State Park in the eastern study area following nest failure, they typically returned to nest in the eastern study area in the following year (Davis et al. 2017, S. Robinson, personal observation). Likely, it is a combination of multiple factors that allowed for positive population growth conditions. The unique circumstances on Fire Island of localized habitat change with a near elimination of red fox may make the results of this study challenging to reproduce (Zharikov et al. 2009). For example, we saw increasing vegetation tolerance by chicks as time since Hurricane Sandy increased, and for plover nests, particularly in 2019 (K. Walker, personal communication). This change may illustrate adaptability in plover habitat use resulting from a shift of the primary predators from foxes early in the study to aerial predators such as peregrine falcons later in the study (Chalfoun and Schmidt 2012). Piping plovers also have high site fidelity (Friedrich et al. 2015, Weithman et al. 2019). Sites that were selected by adults when there was less vegetation cover may have been continually selected for nest and brood rearing sites as vegetation increased, rather than

risking abandoning their territory due to possibilities of increased predation or territorial interactions elsewhere (Catlin et al. 2019).

The best ways to maintain future population growth on Fire Island are to increase habitat to attract immigrants and retain natal recruits in the breeding population, and to prevent the local red fox population from reaching high densities. Ultimately, regardless of the plover breeding stage managed for, reduction in vegetation will increase the amount of available breeding habitat and reduce habitat for terrestrial predators such as red fox. Furthermore, as slope was influential for both chicks and adults, reducing the height relative to the footprint of dunes may improve habitat availability and potentially population persistence (Convertino et al. 2011). The amount of nesting habitat increased on Fire and Westhampton Island following Hurricane Sandy (Walker et al. 2019), but the proportion of the island that was vegetated increased annually (Bellman 2018). Therefore, without intervention or another natural disturbance, the islands may revert to pre-Sandy habitat, which will reduce the carrying capacity of the island and the ability for this small breeding population to act as a source for the surrounding sites.

If the population size in the Fire Island to Westhampton Island study area continues to increase, we may see changes in habitat use. Change may be due to an increase in conspecific attraction if breeding success remains high (Ahlering and Faaborg 2006), or, if habitat suitability declines with increasing vegetation cover, plovers may be forced to settle in less-suitable habitat, as with increasing selection for sites closer to development in plover broods. The dynamics of plover settlement patterns remain an interesting topic for future investigation and bear further study on Fire Island and Westhampton Island.

The persistence of barrier islands means not only the persistence of piping plovers, but also the wide variety of other taxa that use early successional habitats (Maslo et al. 2016). While

stabilizing Fire Island did not stop the population increase of breeding piping plovers in this area, without habitat alteration, there may have been higher densities reached and greater population growth than we observed. However, the restoration areas also supported numerous pairs in later years of this study, likely compensating for some habitat loss to island stabilization. Hardening of shorelines in barrier island systems typically results in a loss of natural dynamics and cumulative land loss (Hein et al. 2019). Further, climate change projections also predict rising sea level, and stabilizing barrier islands reduces the natural adaptability of barrier islands (Moore and Murray 2018). Thus, barrier island stabilization could shift to a living shoreline approach on the mainland to improve natural dynamics and increase resiliency to storms and sea level rise (Bilkovic et al. 2016).

There is more work to be done on the Fire Island and Westhampton Island plover population to understand the long-term effects of Hurricane Sandy, the Fire Island to Moriches Stabilization Project, and predator communities. Although we anticipated the population would reach carrying capacity during the seven years following Hurricane Sandy, we continued to see exponential growth, high reproductive output, and high levels of immigration through the 2019 breeding season. That we detected declines in chick survival and foraging rate, likely as a product of higher nesting density, despite high reproductive output, emphasizes the need for continued monitoring of the population as nesting density increases. For long-term, broad-scale, population enhancement, allowing barrier islands to naturally respond to storm effects should increase the longevity of created plover habitat. In the short-term, before the next major habitat creating event, continued management of plover habitat, particularly vegetation removal, for this population will certainly be needed for the population to continue to grow, or to avoid future declines. Engineered habitat, such as the restoration areas in this study also can work to improve

plover habitat and possibly population persistence in the absence of natural habitat-creating events.

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Appendix I. Confirmation of Copyright ownership of chapter 1



Adele Mullie, Managing Editor,
Biology Dept., Acadia University
Wolfville, NS, Canada, B4P 2R6
mullie@resalliance.org
Ph: 902 585-1313

4 February 2020

Samantha Robinson
Graduate Research Assistant
Virginia Tech Shorebird Program
134 Cheatham Hall
Virginia Tech.

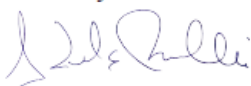
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Sincerely

A handwritten signature in blue ink, appearing to read "Adele Mullie".

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Figure 1. Letter confirming copyright allowance of Chapter 1, 'Irruptions: evidence for breeding season habitat limitation in Piping Plover (*Charadrius melodus*)' from Adele Mullie, Managing Editor.