

2020 Annual Report

Effectiveness monitoring and targeted studies in support of FIMI conservation measures

Piping Plover and Red Fox Monitoring on Fire Island and Westhampton Island, New York

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**This report summarizes Virginia Tech's Effectiveness Monitoring of certain
conservation measures required under the Biological Opinion for the Fire Island
Inlet to Moriches Inlet Stabilization Project.**



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Part 1: Background Information and Introduction

The work described in this report was funded under the Breach Contingency Plan (BCP; USACE 1996), the Fire Island Inlet to Moriches Inlet Stabilization Coastal Storm Risk Reduction Project (FIMI; USACE 2014), the U.S. Fish and Wildlife Service (USFWS) North Atlantic Landscape Conservation Cooperative Beach Resiliency Project (Resiliency Project), and by Virginia Tech. Both the FIMI project and the Resiliency Project were funded under the Disaster Relief Appropriations Act of 2013 (Public Law 113-2). Because these projects were so closely coordinated, we produced one cumulative report in 2019 (Robertson et al. 2019) to provide the best overview of conditions of the piping plover population, the habitat that supports it, and the red fox predator population and its interactions with piping plovers. The U.S. Army Corps of Engineers (USACE) contributions to this project until June of 2015 were made under the Breach Contingency Plan and were restricted to plover studies in the Corps Project Areas. The Resiliency project funding was intended to expand the plover project to include areas of Smith Point County Park in 2013–2016. As continuation of the FIMI funding, our monitoring efforts were meant to continue into 2020. Virginia Tech researchers were unable to conduct fieldwork in 2020 due to university-level travel restrictions associated with the covid-19 pandemic, but land managers at the National Park Service, New York State Parks, and Suffolk County Parks continued piping plover monitoring and data collection in 2020 and shared data with Virginia Tech to be used in this report. Those 2020 data are compiled and are presented here alongside previous years of data and results. Whereas no red fox monitoring was conducted in the field in 2020 due to covid-19, analyses and presentations of findings from prior years were updated and refined. While no inferences or management recommendations changed from the 2019 final report concerning red fox monitoring, the updated analyses, graphics and discussion of management implications are presented in this report.

In 2012, Hurricane Sandy made landfall on the barrier islands of New York and New Jersey and created multiple breaches and overwashes. Three breaches were created within our study area in Fire Island and Westhampton Island: one in the Otis Pike Wilderness of Fire Island National Seashore, one

in Smith Point County Park on Fire Island, and one within Cupsogue Beach County Park on Westhampton Island.

The breaches in the county parks were filled soon after the hurricane in accordance with the BCP. The FIMI project entailed sections of beach and dune construction along the 30.5 km of Fire Island and was initiated by USACE in the winter of 2014. The USACE formally consulted with the USFWS pursuant to the Endangered Species Act of 1973, as amended, due to the potential direct and indirect adverse impacts of these projects on the federally listed species. The USFWS's Biological Opinion (BO) for the BCP covered the piping plover (threatened) and seabeach amaranth (*Amaranthus pumilus*, threatened); the BO for the FIMI included these species as well as the red knot (*Calidris canutus rufa*, threatened; USFWS 1995 and 2014). Anthropogenic alterations to habitat, including dredging, building dunes and intensive human beach use, can reduce plover habitat availability (Cohen et al. 2009, Catlin et al. 2015).

The potential adverse effects of the FIMI on piping plovers listed in the BO included habitat loss and degradation, recreational disturbance, and exacerbation of predation. As a result, the FIMI BO included a number of conservation measures to address these potential effects and reduce the effect of potential incidental take authorized by the USFWS, including inlet-to-inlet monitoring, habitat maintenance and restoration, predator management, and reduction of human disturbance. Vegetation was cleared and the topography was modified by USACE in approximately 33.7 ha (83.2 ac) of ocean-side habitat at Great Gun restoration area to mitigate adverse effects of dune and beach construction. To create possible nesting and foraging habitat for piping plovers, USACE also created New Made restoration area, 6 ha (15.8 ac) of bay-side habitat south of Carter's Island.

Breaches and overwashes can result in creation of new foraging and nesting habitat for piping plover (Cohen et al. 2009, Robinson et al. 2019), but the manipulation of them by dunes built under the FIMI had the potential to disrupt natural plover breeding processes. Thus, the effect of the habitat modifications under the FIMI needed to be monitored and evaluated. Understanding quality of nesting and foraging habitats can lead to a better understanding of the plover response to Hurricane

Sandy and subsequent habitat alterations. The response to habitat change can manifest in changes in demographic rates, growth rates, density, movement, prey abundance, and a variety of other rates (Loefering and Fraser 1995, Elias et al. 2000, Cohen et al. 2009, Catlin et al. 2014, Catlin et al. 2015).

However, plover populations often are affected by predators (Hunt et al. 2019a).

Understanding how the local predator community responds to storm- and anthropogenic habitat alterations, and how the predators are affecting piping plovers during the same period, is necessary to gain the full picture of the effects of habitat change. Red foxes (*Vulpes vulpes*) are a predator of piping plovers on Fire Island (U.S. Fish and Wildlife Service 2014), and in other barrier island ecosystems (Rimmer and Deblinger 1990, Patterson et al. 1991, Cohen et al. 2010, Gieder 2015). Different aspects of red fox population ecology have been studied in a variety of ecosystems (see Lloyd 1980, Ables 1983 for overviews) but changes in occupancy (i.e., presence accounting for detection) have been studied only twice on the U.S. Atlantic Coast, once on Cape Cod, MA and once on Assateague Island, MD (Gieder 2015, O'Connell et al. 2006). No previous monitoring has specifically examined red fox population responses to storm- and anthropogenic habitat alterations nor detailed fox population ecology in a barrier island ecosystem. Land managers frequently undertake both non-lethal (e.g. exclosures) and lethal (e.g. targeted or systematic removal) management of red foxes along the U.S. Atlantic Coast to benefit piping plovers and other imperiled shorebirds and sea turtles (Hunt et al. 2019a). Rarely are the efficiency and efficacy of predation management efforts assessed. There is a growing recognition by managers and the public on the need to monitor and quantitatively assess the success of predation management actions (Hunt et al. 2019a). Thus, the red fox monitoring in the report quantifies occupancy, home range dynamics, numbers, vital rates, habitat selection, movement ecology, and diet of red foxes in plover habitats to best guide predator management efforts.

This report seeks to summarize targeted monitoring programs created to evaluate the efficacy of the BO conservation measures, developed by the USFWS. The monitoring effort seeks to provide a scientific evaluation of the effectiveness of the management and habitat maintenance and restoration

efforts within the FIMI project area and Fire Island, as a whole. Both Virginia Tech and the USFWS worked closely with an interagency team consisting of the National Park Service (NPS), New York State Office of Parks, Recreation, and Historic Preservation, Suffolk County Parks, and the USACE to obtain the necessary permits to undertake this work.

The goal of this project is to provide a broad ecological understanding of how overwashes, breaches, breach fills, and USACE-projects affect piping plover populations, their red fox predators, and their invertebrate prey communities. We compared the dynamics of bird use and invertebrate densities in an open breach area, two filled breach areas, two restoration areas, nine overwash areas, and other pre-Hurricane Sandy habitats within the study area. Ultimately, our results will help to refine our understanding of the timing of and manner in which piping plover habitat develops and persists and how piping plovers respond to habitat creation in the context of predation by a key predator, the red fox.

The report of piping plover monitoring includes the following objectives:

- Objective 1: Compare changes in numbers, density, and distribution of piping plovers in various habitats on Fire Island.
- Objective 2: Compare piping plover nest and chick survival rates in various habitats across Fire Island.
- Objective 3: Compare the relative contribution of local growth (recruitment) vs immigration in population growth associated with new habitats. Determine habitat correlates of population change.
- Objective 4: Compare prey densities at several habitat types.
- Objective 5: Quantify the interactions of predators with shorebird nests and chicks.
- Objective 6: Investigate the potential for applying population models developed by Fire Island to other known and potential plover habitats in Army Corps' project areas.

The report of red fox monitoring includes the following objectives:

- Objective 1: Produce an index of fox abundance to understand the recovery rate of the fox population.
- Objective 2: Estimate red fox reproductive success and relate it to population growth during the recovery from the mange outbreak.
- Objective 3: Quantify the interactions of red fox with shorebird nests and chicks during the recovery from the mange outbreak. Monitor the impacts of foxes versus other predators on plover nests and chicks.
- Objective 4: Use information collected in objectives 1–3 to make recommendations on utility of, and recommend methodologies for, management of red fox populations in the study area and in other coastal habitats.

Study Area

Our study area consisted of 27.1 km of Fire Island and Westhampton Island within the administrative boundaries (referred to as management units in this report) of the National Park Service (Otis Pike Wilderness Area and the Fire Island Lighthouse Tract), Suffolk County Parks (Cupsogue Beach County Park and Smith Point County Park), and the New York State Office of Parks, Recreation, and Historic Preservation (Robert Moses State Park). From 2013 to June 2015, the study area only consisted of Otis Pike Wilderness Area, Smith Point County Park, and Cupsogue Beach County Park (17.3 km of beachfront). In June 2015, when the FIMI funding became available, the study area was expanded to include Robert Moses State Park and the Fire Island Lighthouse Tract (9.8 km; Figure 1). Although we monitored Watch Hill in 2013–2014, the communities between Kismet to Watch Hill were not monitored in later years, thus are not considered a part of our study area. In 2020, the study area only spanned from Robert Moses State Park to Smith Point County Park, no longer including Cupsogue Beach County Park.

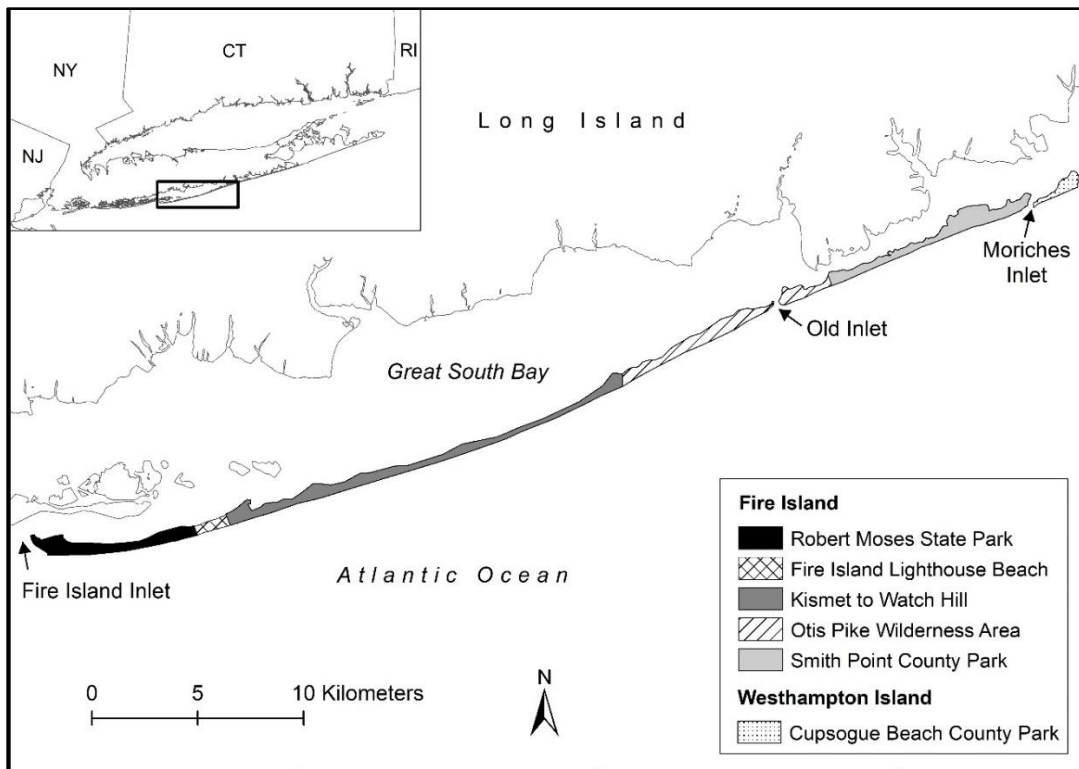


Figure 1. Map of the study area, Fire Island and Westhampton Island, NY comprising different management units.

Prior to Hurricane Sandy, our study area consisted of sandy backshores largely backed by dunes. In October 2012, Hurricane Sandy overwashed several areas of the island. The hurricane created a new breach at Old Inlet, a breach at Cupsogue Beach County Park, and a breach in the Narrow Bay West area of Smith Point County Park. The Old Inlet breach remains open. The Cupsogue breach was filled with a berm 9+ ft. National Geodetic Vertical Datum (NGVD) in elevation, 150 ft. wide and 2000 ft. long (presentation on Coastal Breach Closures, Bocamazo 2013). The Narrow Bay West breach was filled with a berm about 12 ft. NGVD in elevation (based on a completion drawing of Smith Point breach fill, 2013). Prior to the 2015 piping plover breeding season, the USACE constructed two restoration areas to provide potential plover nesting and foraging habitat. This construction consisted of 33.7 ha of flat sand oceanside habitat at Great Gun restoration area, and 6 ha of flat sand bayside habitat at New Made restoration area (hereafter, 'New Made').

Habitats were defined based on USACE polygons of restoration and management areas, post-Sandy delineation of overwash, and Light Detection and Radar (LiDAR) elevation data (Table 1). When possible, we describe landcover characteristics using terminology in Zeigler et al. 2017.

Table 1. Habitat categories used within this report refer to geographic areas on Fire Island and Cupsogue Beach County Park.

Habitat	Definition
Restoration Area	New Made and Great Gun restoration areas, created between the 2014 and 2015 piping plover breeding seasons.
Overwash	Any area that overwashed during Hurricane Sandy. This is a broad category that is subdivided into manipulated or natural overwash.
Manipulated Overwash	Areas of Fire Island that overwashed during Hurricane Sandy, but were manipulated through dune manipulation (including snow fencing and Christmas tree placement), or vegetation management.
Natural Overwash	Areas of Fire Island that overwashed during Hurricane Sandy, but have not been further modified.
Breach Fill	The areas of Fire Island and Cupsogue Beach County Park that breached during Hurricane Sandy, but were filled shortly after by USACE. Both breach fills fall adjacent to manipulated overwashes.
Manipulated Dune	Any dune or berm created by other than natural sources. This includes snow fencing, Christmas trees, planting, and USACE/other engineering.
Management Area	Areas defined by USACE to manage under the FIMI.
Nourishment	Beach widening by the USACE in Smith Point County Park from 2014–2015 and 2018-2019.
Other	A broad category; where the area does not fall into one of the overarching categories above. All following categories could further be defined under the 'other' category, depending on the specificity of the question.
Backshore	The dry sand area between the high-water line and the toe of the dune.
Barrier Interior	The area inland of the toe of the dune and interior of Fire Island.
Swale	A depression or blow-out behind the primary dunes, between ridges; either vegetated or unvegetated.
Beach	The area that is between the high and low water line. Can be further defined as ocean, bay, or inlet depending on the geologic location. Synonymous with the intertidal zone.

Dredge Spoil	Stockpiles and graded areas of dredged sand.
Mud Flat	Mostly intertidal land forms where particles are generally < 0.05 mm in diameter and often mixed with bits of organic material. Areas where fine-grained sediments have been deposited in the low-energy shallows behind the island.
Sand Bar	Mostly intertidal landforms that are generally composed of particles > 0.05 mm. In this study area, sand bars occur north of the inlets.
Flood Shoal	A submerged ridge or bar associated with inlets consisting of or covered by sand; rising from the sea bed to near the surface so that it is tidally exposed. They are often not static and may move seasonally and annually.

We divided the site into smaller subsites intended to be relatively homogeneous in geomorphological and ecological structure (e.g., areas where overwash occurred were distinct from highly vegetated tall dunes, Table 2, Figure 1, Figure 2, Figure 3). These subsites allowed for general location referencing when GPS accuracy was not required. Monitoring surveys were performed by subsite.

Table 2. Subsite names, location descriptions, and habitat on Fire Island and Westhampton Island, 2013–2020.

Name	Subsite Code	Description	Habitat Type
Democrat Point	DMP	Begins at federal navigation channel stone jetty on bay and ocean side at the west ends of OSS and STP, and extends west to the inlet.	Beach, Backshore, and Interior
Ocean South Side	OSS	Begins at blue hut at the west end of Field 3 and extends west to the western stone jetty on the ocean side.	Beach, Backshore, Interior, and Swale
Stockpile	STP	Sand stock pile area on bay side of island; begins at west end of golf course and extends west to the northernmost point of the rock jetty.	Dredge Spoil, Beach, Interior

The Golf Course	GOLF	Begins at west side of the Field 2 parking lot behind the primary dune line and extends west to the beginning of the sand stock pile area and north to the major roadway. Not plover habitat.	Golf course
Field 3	FLD3	Begins at blue hut to the west end of Field 4 and extends west to the next blue hut in front of the Field 2 parking lot.	Beach, Backshore, and Interior
Field 4	FLD4	Begins at blue hut to the west end of Field 5 and extends west to the next blue hut in front of the Field 3 parking lot.	Beach, Backshore, and Interior
Field 5	FLD5	Begins at signage at the west end of Fire Island Lighthouse and extends west to the blue hut at the boundary of Field 4.	Beach, Backshore, and Interior
Fire Island Lighthouse	FIL	Fire Island Lighthouse Tract of NPS; begins at eastern edge of sand ORV track running inland before Kismet community housing begins and extends west to signage indicating the boundary with Robert Moses State Park.	Beach, Backshore, Interior, Swale, and Manipulated Dune
Watch Hill	WHL	Begins at Watch Hill and extends east to Bellport Beach.	Beach, Backshore, Interior, and Natural Overwash
Old Inlet West Reference	OIWR	Stretch of beach between the east end of Old Inlet West and Bellport Beach.	Beach, Backshore, Interior, and Natural Overwash
Old Inlet West	OIW	Begins at west side of Old Inlet and extends to the point where large primary dunes begin.	Beach, Backshore, Interior, and Natural Overwash
Flood Shoals	FS	Flood shoals associated with Old Inlet.	Flood shoals
Old Inlet East	OIE	Begins where the primary dune line ends and extends west to Old Inlet.	Beach, Natural Overwash, and Interior
Bridge West	BRW	Stretch of backshore with primary dune line between Bridge Overwash and Old Inlet East.	Beach, Backshore, and Interior
Bridge Overwash	BRO	Overwash in the Otis Pike Wilderness, just west of the NPS Visitor Center.	Beach, Natural Overwash, and Interior

Bridge East	BRE	Begins where the primary dune line begins at west end of Pattersquash Overwash and extends to the Otis Pike Wilderness at NPS Visitor Center.	Beach, Backshore, and Interior
Pattersquash Overwash	PSO	Overwash west of Pattersquash East.	Beach, Manipulated Overwash, Interior, and Manipulated Dunes
Pattersquash East	PSE	Stretch of backshore with primary dune line between Narrow Bay West and Pattersquash overwash.	Beach, Backshore, and Interior
Narrow Bay West	NBW	Includes the overwash and small breach-fill west of the Hazardous Area.	Beach, Manipulated Overwash, Interior, Manipulated Dunes, and Breach Fill
New Made	NMA	Begins at the east end of the filled dredge spoil and extends west to the east edge of the small breach-fill.	Beach, Backshore, Manipulated Dune, Interior, and Restoration Area
Narrow Bay East	NBE	Begins at the westernmost end of the large dune and extends to the westernmost end of the Hazardous Area.	Beach, Manipulated Overwash, Interior, and Manipulated Dunes
Smith Point West	SPTW	Begins at Cut 3 on Burma Road and extends to the end of the large dune and beginning of the Narrow Bay East manipulated overwash area.	Beach, Backshore, and Interior
Smith Point East	SPTW	Begins on west side of Moriches Inlet and extends west to Cut 3 on Burma Road.	Beach, Backshore, Manipulated Dune, Interior, and Restoration Area
Cupsogue West	CSW	Breach-fill and Moriches Inlet area of the Cupsogue Beach County Park. Begins at the west edge of the breach-fill and extends west to Moriches Inlet.	Beach, Manipulated Overwash, Manipulated Dunes, Interior, and Breach Fill
Cupsogue Sandbar	CSB	Large sandbar/shoal north of Cupsogue West.	Sand Bar

Cupsogue East	CSE	Beach and narrow strip of bayside intertidal zone at east end of the Cupsogue Beach County Park. Begins at the west end of the parking lot and extends west to the east edge of the breach-fill.	Beach, Backshore, Manipulated Dune, and Interior
Cupsogue Mud Flats	CMF	Mud flats north of the Cupsogue parking lot, and south of the high bare Island in Moriches Bay.	Mud Flat

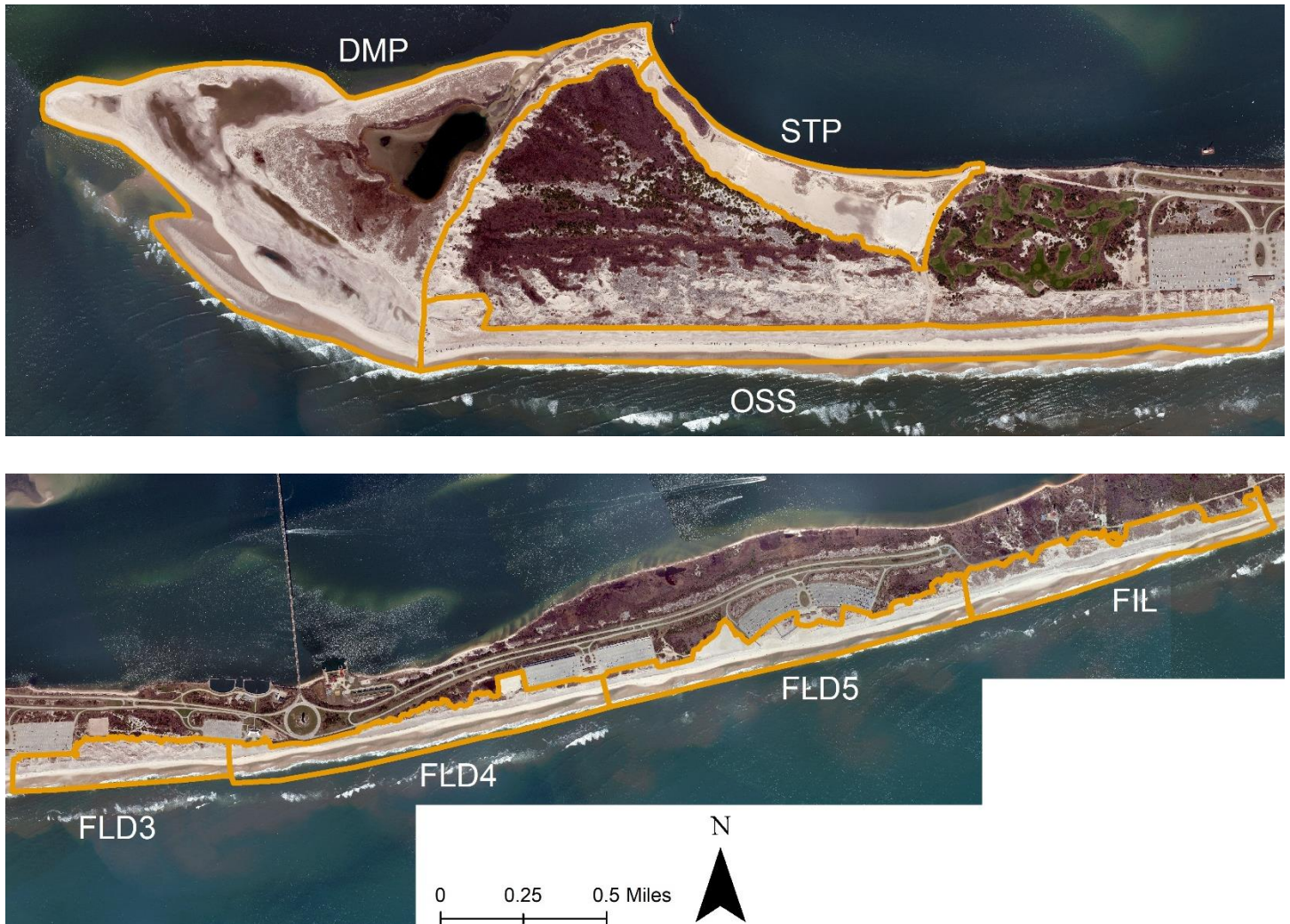
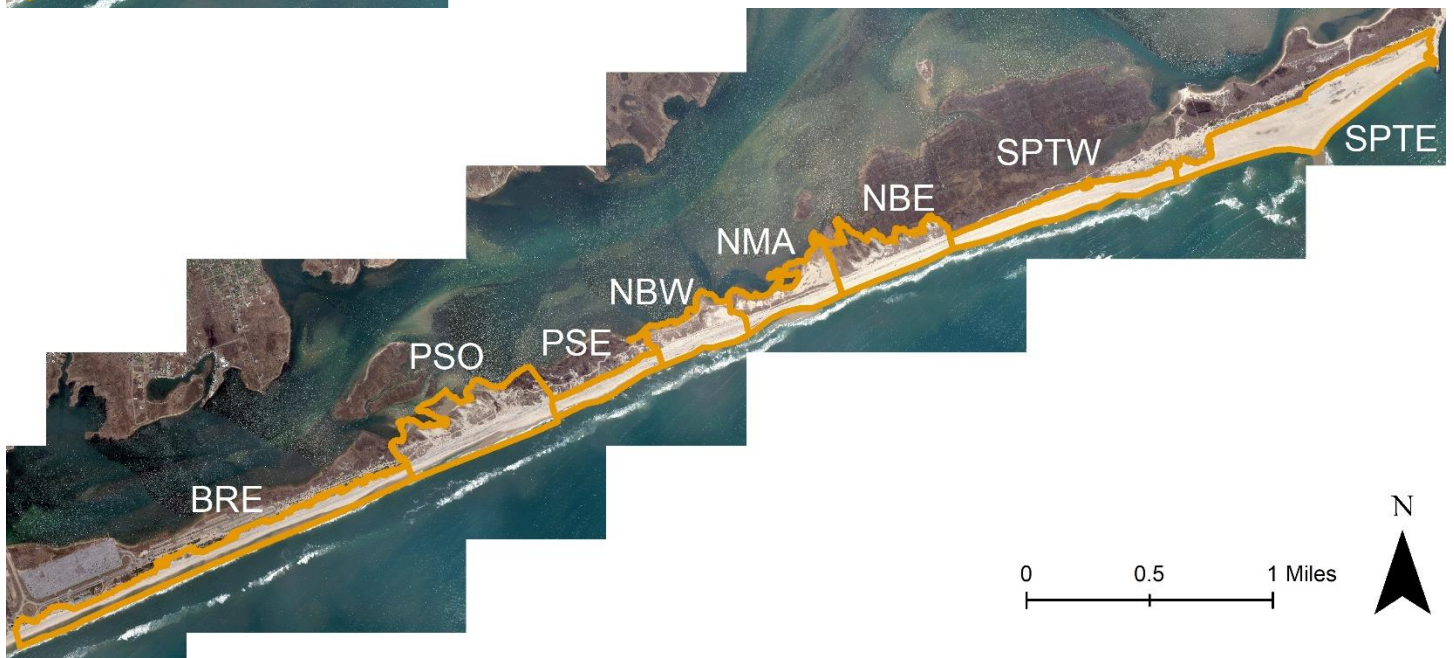
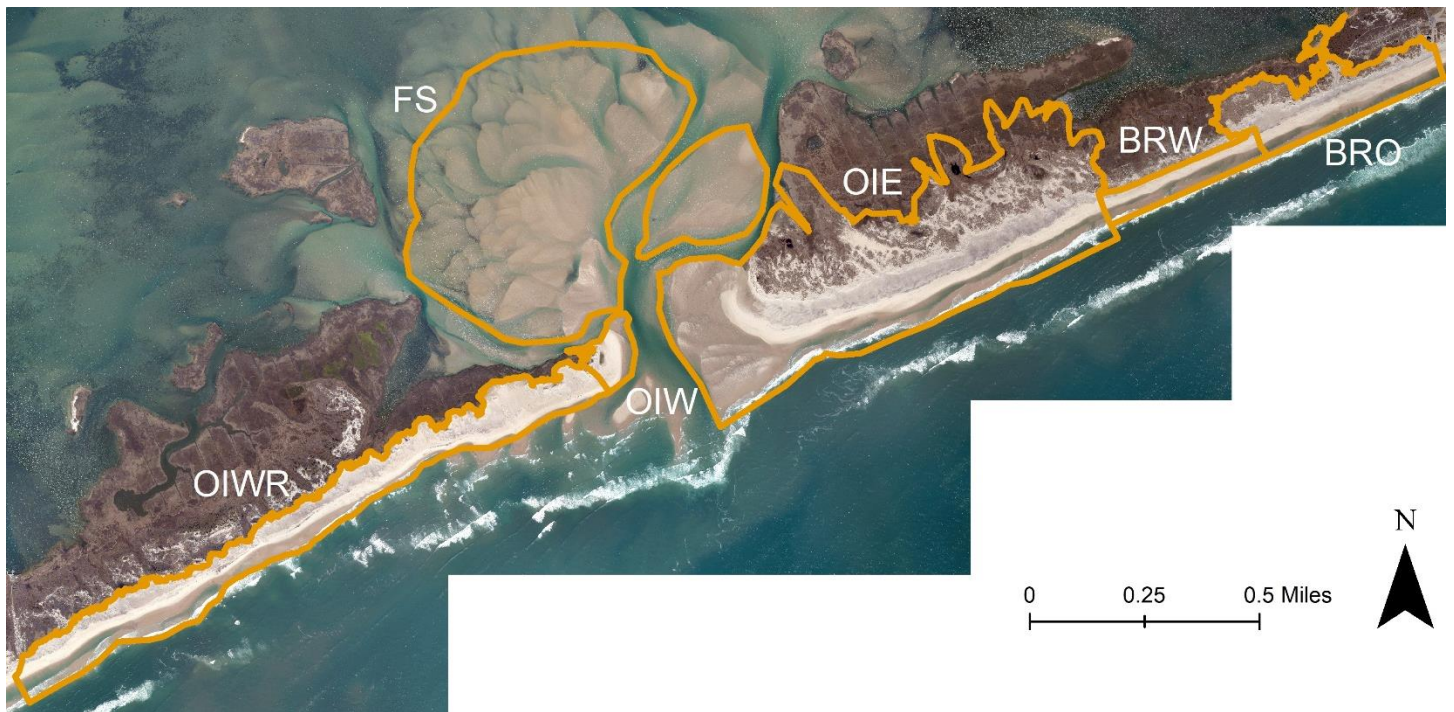


Figure 2. Study area at Robert Moses State Park (top and bottom) and Fire Island Lighthouse Tract (bottom). Subsite boundaries are outlined in orange. See Table 2 for subsite names and descriptions. Imagery captured April, 2020.



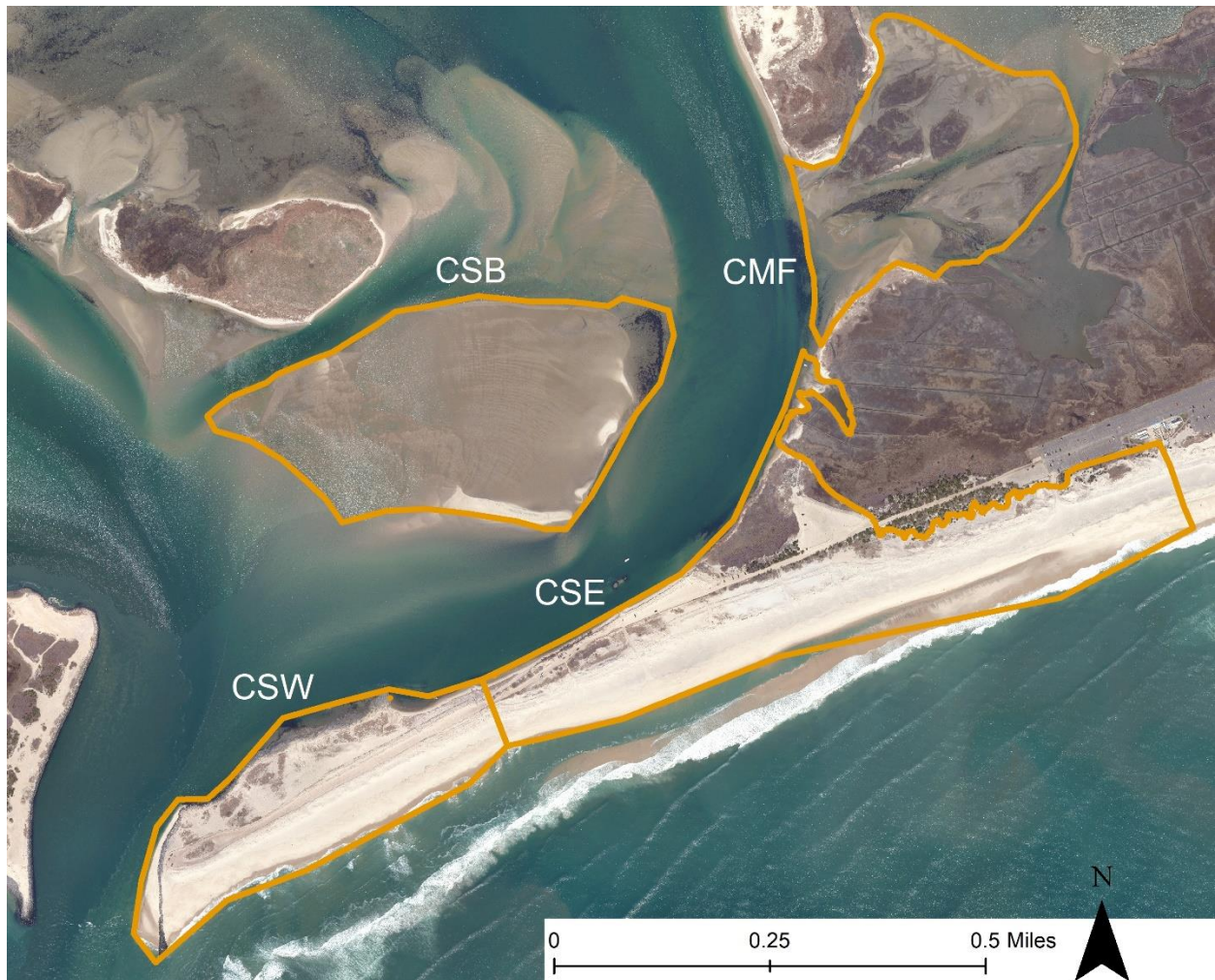


Figure 3. Study area at Otis Pike Wilderness Area Park (top), Smith Point County Park (middle), and Cupsogue Beach County Park (bottom). Subsite boundaries are outlined in orange. See Table 2 for subsite names and descriptions. Imagery captured April, 2020.

Throughout the plover breeding seasons, all beaches were open to pedestrians. Smith Point County Park and Robert Moses State Park also allowed recreation vehicles to drive onto the beaches. Every year, these beaches were closed to vehicles once chicks hatched and were re-opened once chicks fledged (Table 3). However, Smith Point County Park in 2013, and subsite OSS in Robert Moses State Park - South in 2017–2019, remained open to vehicle access following piping plover hatch dates. Official dates of closures for 2013 are uncertain. Despite vehicle closure to the general public, law enforcement, park staff and plover monitors were still permitted to drive through closed areas, depending on the circumstance.

Table 3. Beach closure dates for vehicle use at Smith Point County Park and Robert Moses State Park 2013–2020.

Management Unit	2013	2014	2015	2016	2017	2018	2019	2020
Smith Point County Park	closed, but dates unknown	09 Jun–01 Aug	09 Jul–13 Aug	22 May–25 Aug	27 May–05 Aug	11 Jun–21 Aug	23 May–9 Aug	May 21–Aug 27
Robert Moses State Park - North	-	-	06 Jun–04 Aug	06 Jul–22 Jul	07 Jun–16 Jul	02 Jun–03 Aug	06 Jun–13 Jul	29 May–22 Jul
Robert Moses State Park - South	-	-	10 Jul–04 Aug	25 Jun–05 Aug	24 May–10 Aug	29 Jun–03 Aug	04 Apr–end of season	Apr–end of season

Part 2: Piping Plover Monitoring on Fire Island and Westhampton Island

Section 1: Field Methods

Habitat and Tide Mapping

In 2013 and 2014, we collected all mapping data with a Garmin 78 (Garmin International, Olathe, KS). We used a Trimble Geo7x (Trimble Navigation, Ltd., Sunnyvale, California, USA) in 2015–2019 to map the shoreline during spring high and low tides along the bay and ocean beach (Figure 4). Tides were mapped at the shoreline throughout the entire season, although no low tide data was collected in 2014. In 2015, we mapped spring high tide and low tides during mid-May and early June, and mapped various habitats and subsite boundaries during late July and early August. In 2016, we mapped shorelines at spring high tide and low tides May–September, and completed snow and symbolic fencing mapping during late-July and August. In 2017, we mapped the shorelines during spring high and low tides in May, and the snow and symbolic fencing during late June–August. In 2018, we mapped shorelines at spring high and low tides in May and June, and mapped snow and symbolic fencing May–August. In 2019, we mapped shorelines at spring high and low tides in May and June, and mapped snow and symbolic fencing April–July. No tide lines were mapped in 2020.



Figure 4. Using a Trimble Geo7x to map the spring tides by walking along the high-water line.

Adult Survey

We surveyed each subsite in the study area for adult piping plovers every 1–3 days, April–August, 2013–2019. We surveyed subsites on foot and by UTV. Some subsites that did not have bayside habitat and consisted only of narrow ocean beach were surveyed by driving a UTV slowly along the ocean beach and along the backshore. UTVs were only driven outside of areas protected by symbolic fencing established by land managers. At least twice per week during the nesting period (April–July), we surveyed by foot to search for plover tracks, scrapes, and nests. When conducting foot surveys, observers walked parallel tracks 50–100 meters apart depending the size of the subsite, facing either east or west. Transect width varied depending on topography, vegetation, weather conditions, and other factors affecting visibility. If the entire width of the subsite could not be surveyed in one pass, observers conducted multiple passes of the subsite walking parallel transects. Monitors carried spotting scopes (20–60x, 80 mm) to resight plovers (Figure 5). Upon sighting a plover, we recorded its band combination (if banded), behavior, and habitat. In 2013–2015, we recorded the location of individuals with a Garmin GPS unit. In 2016–2019, we used a Nikon laser rangefinder and a Trimble GPS unit to record the location of plovers (Robinson et al. 2020a). In 2020, land managers from the National Park Service, New York State Parks, and Suffolk County Parks surveyed nesting areas and resighted banded adults as often as possible, but resight effort was not consistent with that of 2013–2019.



Figure 5. Surveying for piping plovers using spotting scopes inside the Great Gun restoration area at SPTE.

Nest Locations

We searched all potential nesting areas in the study area, including backshore, overwashes, and sparsely vegetated areas. During 2013–2019, we searched nesting areas every 1–3 days. Nest locations were recorded using a Garmin GPS unit (2013–2014) or a Trimble GPS (2015–2019, Figure 6a) unit. If a nest was found at full clutch, we floated all four eggs to estimate the initiation and hatch date (Alberico 1995; Figure 6b). In 2020, local land managers conducted nest searches and collected nest locations through NestStory (National Park Service), handheld GPS (Suffolk County Parks), and by digitizing them into Google Earth based on geography and land markers (New York State Parks).



Figure 6. a) Using a Trimble Geo7x to map the location of a piping plover nest. b) Floating an egg from a four-egg nest in SPTE.

Nest Checks

During 2013–2019, we checked nests every 1–3 days throughout the incubation period (Figure 7). In 2020, land managers checked nests as frequently as possible, ideally every 1–3 days. As the hatching date approached, nests were checked for signs of hatch approximately every day. Nest fate was determined from observations of the nest and surrounding area.



Figure 7. a) Checking an exclosed nest for hatch using binoculars. b) Checking an unexclosed nest for hatch.

Trapping and Banding

During 2013–2019, we attempted to trap banded and unbanded adults during the incubation period, over a full clutch, using a drop-box trap or shoo-in funnel trap. Once captured, plovers were removed from the trap, banded, weighed, and measured (Figure 8a). If the second adult of a particular nest had not yet been trapped that year, we reset the trap while processing the first adult. We attempted to capture banded plovers to assess the condition of bands, flags, and leg health. If no adults entered a trap within 20 minutes of its deployment, we removed the trap and did not return to the nest that day. We captured, banded and processed plover chicks on the initial nest visit post-hatching (Figure 8b) and recaptured them at a minimum of 20 days post-hatch to weigh and measure them a second time. No adults or chicks were captured nor banded in 2020.

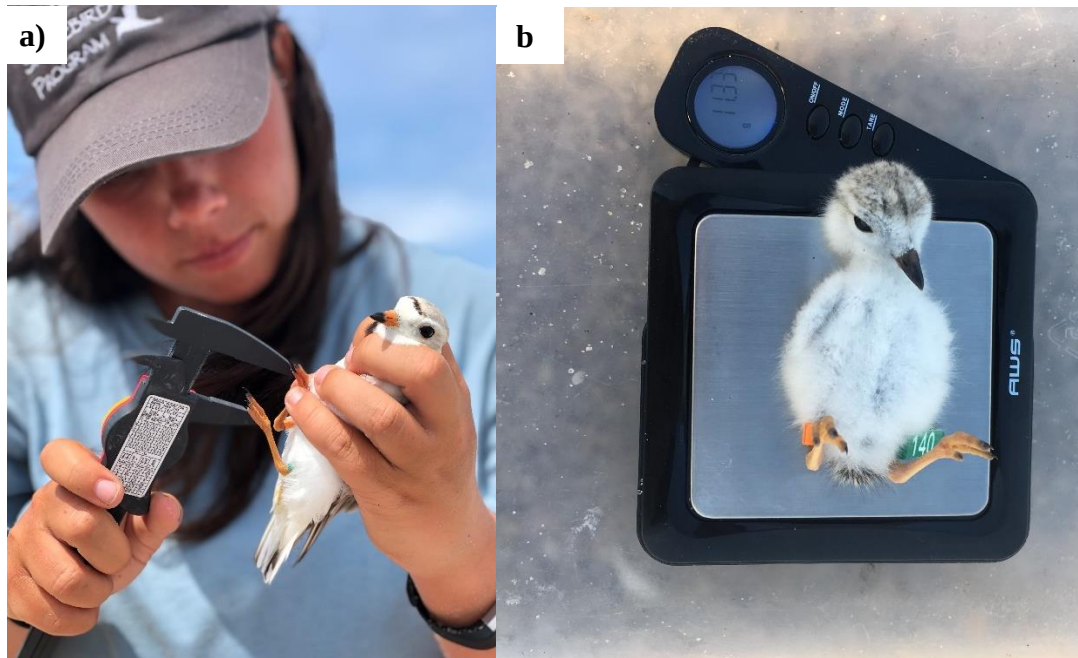


Figure 8. a) Measuring the tarsus of an adult piping plover. b) Taking the mass of a 10-day old chick.

Banding Schemes

In 2013, some birds received two color bands on each upper leg or green flags with alphanumeric combinations with a yellow band on the opposite leg (DeRose-Wilson et al. 2013, 2014). During 2014–2019, we banded all adults and chicks with dark green flags with a three-digit alphanumeric ID etched in white on one upper leg and a numbered orange Darvic band on the opposite upper leg (Figure 9).

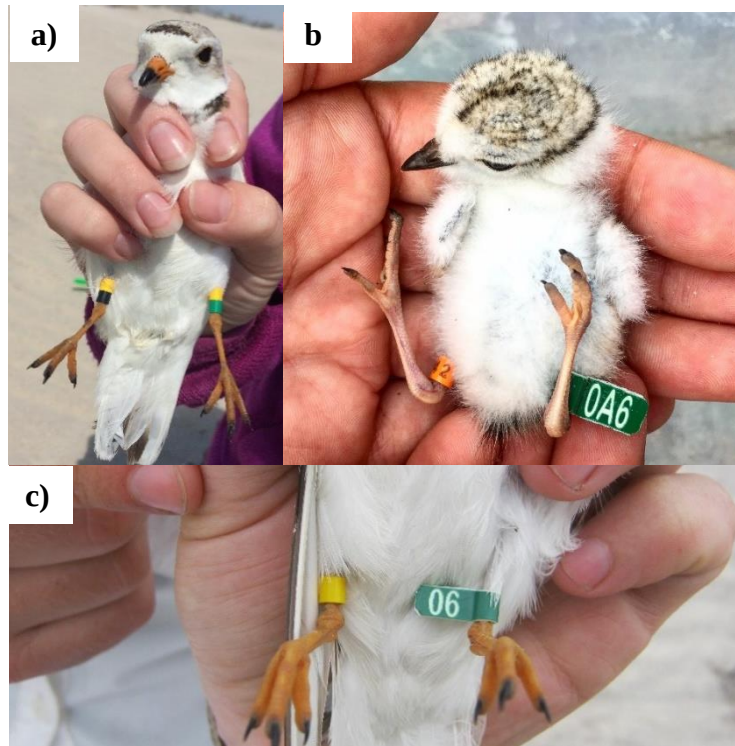


Figure 9. a) A piping plover adult with two color bands on each upper leg, b) a chick banded with a green alphanumeric flag and an orange color band, and c) an adult with a green alphanumeric flag and a yellow color band.

Brood Observations

During 2013–2019, we searched for plover chicks for 30 days post-hatching, regardless of brood fate. If weather permitted, we visited broods at least every three days. During 2020, broods were visited by local land managers as often as possible until chicks were confirmed as fledged. During 2013–2019, we attempted to collect a behavioral sample on at least one randomly selected chick in each brood during every visit. To determine the start time of the behavioral sample after locating a brood and to randomly choose a chick, we used a random number generator. For five minutes, we recorded forage rate (peck, pull, probe) continuously and behavioral state (forage, sit, run, walk, chase, flee, preen, encounter with another individual) and habitat (moist sand, moist vegetation, dry sand, dry vegetation, and wrack) every ten seconds (Altmann 1974). We conducted a disturbance point count for which we recorded the presence of anything other than the brood (humans, vehicles, predators, competing piping plovers, etc.) within 100 m of the observer for five

minutes, noting their location relative to the brood. If more than one observer was present, we conducted the behavioral sample and the disturbance point count simultaneously; if only one observer was present during the brood observation, we conducted the disturbance point count immediately after the behavioral sample. If the brood moved more than 100 m during the observation we randomly selected another chick and conducted a behavioral sample at the new location. No brood observations or disturbance samples were taken in 2020.

Invertebrate Sampling

We sampled terrestrial invertebrates from 2014–2019 in various habitat types (backshore, overwash, breach fill, restoration area, beach) from the time that the first chicks hatched until the time the last chicks fledged. We collected four samples during each invertebrate sampling set. Two of these samples were taken on the beach and two were taken at randomly selected locations within the subsite. For the beach samples, we followed a transect parallel to the beach just above the intertidal zone. Using a Garmin GPS unit, we navigated to the last data point collected on the beach during the previous sampling set in the subsite. From there, we continued along the beach a randomly generated number of meters, from 1–50, to arrive at the location of the first sample in our current sampling set. We walked 50 m along the beach for the subsequent sample. The third and fourth samples for the set were chosen from a predetermined, random selection of points within 100 m of the previous sample. We sampled invertebrates using two paint stirrers coated with Tanglefoot Tree Insect Barrier (Tanglefoot Company, Grand Rapids, Michigan). One paint stirrer was coated on one side with Tanglefoot and placed flat on the sand, Tanglefoot side up. The second paint stirrer was coated on both sides with Tanglefoot and positioned vertically in the sand. The sticky area on the horizontal paint stirrer was 64.5 cm² and 129 cm² on the vertical. We placed a cage over the trapping station to prevent any birds from getting stuck in the Tanglefoot (Figure 10). We returned to each sample location after 30 minutes and counted, measured (± 1 mm), and identified any arthropods stuck on the paint stirrers to order.



Figure 10. Invertebrate trapping station with a vertical and horizontal paint stirrer coated in Tanglefoot placed in a wire cage.

Nest Cameras

In 2016–2019, we placed remote cameras (Reconyx Rapidfire, RC60 Covert IR, Holmen, WI, USA) at nests to detect anything that visited the nest enclosure. No nest cameras were placed in 2020. All cameras were placed in a camouflaged box for theft protection. We programmed the cameras to have a 5-minute picture interval, and take 3 pictures per trigger with a 5 second delay after each trigger. To reduce the chance that a camera would cause a decrease in nest survival, we only placed cameras at exclosed nests. Cameras were installed once we successfully trapped both adults and the nest reached a full clutch. Before installing the camera box, we made observations of piping plover tracks surrounding the nest enclosure, and chose an area that did not appear to be heavily used by adults entering or exiting the enclosure. When installing the cameras, our first priority was to place the boxes in low-traffic area to reduce camera-caused disturbance. Our second priority was to face the boxes north or south to avoid having them face directly towards the sun, preventing overexposure. We placed the camera box against the outside of the enclosure and aimed the camera toward the nest. We attached the camera box to the enclosure with a bungee cord to secure it in place (Figure 11). We performed any maintenance needed to cameras, such as replacing memory cards and

batteries, while we conducted daily nest checks to reduce disturbance. The cameras were removed when the nest failed or the brood permanently left the enclosure area.



Figure 11. A remote nest camera installed outside of a nest enclosure and potentially capturing photos of a snowy owl.

Section 2: Classification Methods

Each year, a raster of classified habitat types was created from annual high-resolution (15-cm) aerial imagery with 4 bands (R, G, B, NIR), using ArcGIS Desktop 10.6 Interactive Supervised Classification (Maximum Likelihood Classification). Training samples were selected for dry sand, vegetation, wet sand, and water. Interactive Supervised Classification is an iterative process which allows refinement of the classification results. Even with this, there was a great deal of overlap in band reflectance of vegetation, water, wet sand, dark sand, and shadows. The human brain is adept at perceiving whether a pixel classified as water is actually the shadow of a tree but numerical models, as yet, are not capable of making those distinctions. In order to use these habitat classifications for modeling, various methods in ArcGIS were used to reclassify pixels which were misclassified in the initial classification of the whole island, for example, pixels classified as vegetation on the beachfront or pixels classified as wet sand or water in dry areas of the island interior.

In order to reclassify large, uniform classes on the landscape (such as beachfront dry sand), we created a polygon shapefile over the area. A value field was added to the shapefile attribute table and given a numeric value equal to the desired class. The polygon was converted to a .tiff raster of the desired class by using the Polygon to Raster tool and then merged to the habitat classification. A second method to correct misclassified pixels was to clip an area of the original classified raster (Clip) and then reclassify certain pixel classes (Reclassify). This method was used to clip the interior of the island where water and wet sand are known to be absent and reclassify those pixels as vegetation.

In addition to correcting and masking misclassified pixels, a raster of water and intertidal sand was classified from DEM (digital elevation model) data on the ocean side of the island and bayside overwashes. The oceanfront intertidal range was 0–4.11 ft in elevation, based on the Astronomical High Water at NOAA Moriches Inlet tidal station. The bayside intertidal range was 0–1.46 ft in elevation, based on mean high water at NOAA Smith Point Bridge tidal station. We reclassified each DEM to select pixels within both the oceanfront and bayside intertidal and subtidal range. These pixels were reclassified with numeric values to represent intertidal wet sand and water, respectively.

The refined layers from each of these methods were superimposed over the original maximum likelihood classification, masking the misclassified pixels.

Section 3: Compare changes in numbers, density, and distribution of piping plovers in various habitats on Fire Island

Introduction

Hurricanes, wildfires, and other disturbance events are important drivers of ecological processes and creators of habitat heterogeneity (Turner 2010). Processes such as overwashing and breaching, that occur because of high surges during storms like Hurricane Sandy, often result in the creation of new, early successional habitats by removing or burying vegetation and creating bayside sand flats (Robinson et al. 2019). Such habitats are utilized by at-risk species such as the Atlantic Coast piping plover (Cohen et al. 2009, Walker et al. 2019).

Habitat changes resulting from anthropogenic and natural forces affect piping plover population dynamics (Cohen et al. 2009, Catlin et al. 2015). Many plover populations are regulated by density dependent forces on the breeding grounds (Cohen et al. 2009, Catlin et al. 2019a). There is evidence that adult survival, breeding propensity, nest survival, and chick survival are reduced when nesting densities are high (Weithman et al. 2017, Hunt et al. 2018a). Lower densities may reduce intra- and inter-specific competition among individuals for nesting and foraging space. Reduced competition for space and thus an increase in available nesting and foraging territories may lead to a population increase in density-dependent species, and has been observed in piping plover on several occasions (e.g., Wilcox 1959, Cohen et al. 2009, Catlin et al. 2015, Hunt et al. 2018a, Robinson et al. 2019). Given the increase in habitat following Hurricane Sandy, a similar process was predicted to unfold in the piping plover population on Fire and Westhampton Islands.

Disturbance and the subsequent habitat creation following Hurricane Sandy had the potential to lessen the negative feedback from density-dependent processes acting on the Fire and Westhampton islands plover population by increasing the amount of habitat available, and thus presented an opportunity to investigate these processes. With the addition of the breach fills and restoration areas, we were able to assess how plovers used natural and human-created habitats and how plover abundance changed following their creation. Specifically, we investigated how these

processes interacted with the changes in piping plover abundance, density, and distribution following Hurricane Sandy. To test whether plover populations on Fire and Westhampton islands were density dependent, we monitored changes in population size, availability habitat, and density following Hurricane Sandy. If plovers are regulated by density dependent factors, we expected to see plover numbers quickly increase in response to the new available habitat and then eventually stabilize around carrying capacity (Wilcox 1959, Cohen 2009, Robinson et al. 2019).

Methods

Using color bands and field-readable, alphanumeric ID flags, we banded adults and chicks from 2013–2019. Our goal was to capture every unbanded plover each year to help us identify individuals for a variety of analyses. In particular, if we could capture the majority of unbanded adults and chicks in each year, we could understand the contribution of immigration to our study area from each origin class (e.g. natal recruits, immigrants). No unbanded birds were banded in 2020.

We compared the number of pairs that used various habitats during 2013–2020, including backshore, restoration areas, natural overwashes, and manipulated overwashes to determine if plovers were using any of these newly created habitats more often than habitats that were available before Hurricane Sandy (see Table 1 for habitat definitions). Using the GPS locations collected at every nest, we assigned nests a discrete habitat type and compared the proportion of nests that occurred in each of those habitat types. We assumed that if a male renested in the same subsite or habitat type, the location of the renest was not independent of the first nest. We only included renests of stable pairs (same male and female) in the habitat-specific pair counts if their new nest was in a different subsite or different habitat class.

We estimated annual pair numbers using the males within pairs. We used males for pair counts and productivity estimates because when pairs separate, the males often keep their territory when they partner with a new female. Additionally, males are the primary territory holders and defenders (Haig and Oring 1988). Using banded adult information and nest date overlap, we used the highest

number of male territories per management unit each breeding season as an estimate of the number of pairs in that unit. To account for pairs that included unbanded individuals, we used the initiation and failure dates to determine if the pairs were independent from individuals banded later in the season. We used this estimate to avoid double counting any male that nested more than once in a management unit, resulting in a conservative pair estimate.

We monitored nests each year for success and to determine the cause of any nest failure. Nests were assigned a fate of successful if they hatched at least one chick and failed if they were abandoned, depredated, flooded, or suffered total egg loss that was not due to hatch. Any time an egg was missing during a routine nest check, we attempted to determine the cause of egg loss. In most cases, egg loss could be attributed to hatch and chicks were present to confirm the nest fate. In cases where no chicks were present, we assigned the nest a fate based on any sign we could find near the nest including mammal or avian tracks (predation), egg yolk (predation), sand erosion from high water (flooding), etc. If a nest disappeared with no discernable sign of fate, we assigned it an unknown fate. If a nest seemed to be abandoned, we looked for any sign that an adult was incubating the eggs for three or more consecutive visits over six days. After six days, if there was no sign of an adult tending the eggs, we assigned the nest as abandoned.

Nests also were given a habitat designation depending on their habitat type and geologic location on the island. The habitats assigned included swale, natural overwash, manipulated overwash, dune, manipulated dune, barrier interior, backshore, or restoration area. Nests and their associated breeding pairs were then regrouped into overwash, breach fill, restoration area, or backshore/barrier interior to compare how many pairs nested in newly created habitat versus previously available habitat. Overwashes, breach fills, and restoration areas all represent new habitats created after Hurricane Sandy. The USACE provided polygons delineating restoration areas (USACE 2014), and we generated polygons to delineate all additional post-Hurricane Sandy habitats. Backshore/barrier interior was habitat available to plovers before the overwashes and breaches occurred in 2012. Natural overwash was only assigned to a nest if it was within the original, Hurricane Sandy-created

overwashes. Nests found in overwashes created after Hurricane Sandy were given a habitat designation other than natural overwash.

We estimated nesting plover pair density by subsite, management unit, and total study area for all years 2013–2020. Using our delineated subsites, extending from the ocean to the bay, we calculated the hectares of dry sand in each subsite (Part 2, Section 2). Using the Region Group tool in ArcGIS, we calculated 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. We assessed density using the total number of pairs that nested in the study area, management unit, or subsite. Pair counts were obtained from Robert Moses and Fire Island National Seashore staff for 2013 and 2014 in Robert Moses State Park and the Fire Island Lighthouse. Pair counts for 2020 were provided by Robert Moses State Park, the National Park Service, and Suffolk County Parks. For subsite density, we grouped OSS and STP to allow for comparisons of island-cross sections. For management unit density, we grouped the Fire Island Lighthouse Tract with Robert Moses State Park, as no perceivable barrier to piping plover movement was detectable between the two management units. We compared the density between subsites that had direct bay access (DMP, OSS-STP, PSO, NBW, and CSW) and subsites that did not have direct bay access. We used the estimated densities to test for a relationship between reproductive output and density in Part 2, Section 3.

Results

Between 2013 and 2019, we banded 241 adult piping plovers (128 females and 113 males) and 765 chicks (Table 4). All chicks were banded between 0 and 16 days old. In 2013 and 2014, eight nests were found at Watch Hill. Five adults and three chicks from those nests were banded. We did not monitor nests at Watch Hill from 2015 through 2019 due to logistical limitations, but these areas were continually monitored by the National Park Service. We did not band any birds at Robert Moses State Park or the Lighthouse Tract in 2013 and 2014 as we did not begin work at those sites until 2015. No birds were banded in the 2020 breeding season. Of the 765 total chicks banded, 4.4% were banded in

the 2013 season, 5.4% in 2014, 6.1% in 2015, 13.2% in 2016, 17% in 2017, 22.1% in 2018, and 31.8% in 2019.

Table 4. Piping plover adults and chicks banded on Fire Island and Westhampton Island during 2013–2019 per management unit. within each management unit are abbreviated in parentheses. See Table 2 for detailed description of subsites.

Management Unit	Adults		Chicks
	Females	Males	
Cupsogue Beach County Park (CSE, CSW)	23	16	126
Smith Point County Park (BRE, PSO, PSE, NBW, NMA, NBE, SPTW, SPTE)	38	36	286
Fire Island National Seashore - east of breach (OIE, BRO)	17	17	138
Fire Island National Seashore - west of breach (OIW, OIWR)	4	6	42
Fire Island National Seashore - Lighthouse Tract (FIL)	4	4	11
Robert Moses State Park (FLD5, FLD4, FLD3, OSS, STP, DMP) ^a	40	31	159
Outside Study Area - Bellport to Watch Hill ^b	2	3	3
Total	128	113	765

^a Birds were only banded from 2015–2019.

During 2013–2020, we located and monitored 449 nests (Table 5, Table 6). Of these nests, 299 (66.6%) hatched and 150 (33.4%) failed (Table 5, Table 6). Depredation and abandonment were the two largest causes of nest failure at 13% and 12%, respectively (Table 6). The highest abandonment rate was in 2014, at 20%, and the greatest depredation rate was in 2015 (46%). Of the 2015 nests, 18 were believed to have been depredated by red fox at Smith Point County Park based on fox sign found at the nest site. At least one fox had learned to enter exclosures at Smith Point by tearing the netting at the top to get to the eggs inside, leading to the removal of exclosures from nests, which all subsequently were depredated.

Land managers found 74 nests in 2020; 62 survived to hatching and 12 failed (Table 6). Of the 12 nests that failed, seven were abandoned, two were depredated, one flooded, and two fates were unknown. Both nests depredated in 2020 were unexclosed and both were in manipulated overwashes (Table 7).

Table 5. Piping plover nest distributions and status within Fire Island and Westhampton Island study area, in various habitats of each management unit, 2013–2020. Nest numbers include renests of some pairs. Nests were only designated as within natural overwash if they were within original Hurricane Sandy-created overwashes.

Management Unit	Habitat	Found	Hatched	Failed	Hatch %	Fail %
Fire Island National Seashore - Lighthouse Tract ^a	Backshore	1	1	-	100	-
Fire Island National Seashore - Lighthouse Tract ^a	Barrier Interior	2	-	2	-	100
Fire Island National Seashore - Lighthouse Tract ^a	Manipulated Dune	2	2	-	100	-
Fire Island National Seashore - Lighthouse Tract ^a	Swale	1	1	-	100	-
Robert Moses State Park ^a	Backshore	74	52	22	70	30
Robert Moses State Park ^a	Barrier Interior	15	7	8	47	53
Robert Moses State Park ^a	Dredge Spoil	6	4	2	67	33
Robert Moses State Park ^a	Swale	6	4	2	33	67
Robert Moses State Park ^a	Dune	4	3	1	75	25
Robert Moses State Park ^a	Management Area	1	1	-	100	-
Cupsogue Beach County Park ^b	Backshore	6	4	2	67	33
Cupsogue Beach County Park ^b	Barrier Interior	11	7	4	64	36
Cupsogue Beach County Park ^b	Manipulated Dune	3	3	-	100	-
Cupsogue Beach County Park ^b	Manipulated Overwash	35	24	11	69	31
Fire Island National Seashore - east of breach	Manipulated Dune	1	-	1	-	100
Fire Island National Seashore - east of breach	Natural Overwash	61	43	18	70	30
Fire Island National Seashore - east of breach	Backshore	1	1	-	100	-

Fire Island National Seashore - west of breach	Natural Overwash	17	13	4	76	24
Smith Point County Park	Backshore	25	15	10	60	40
Smith Point County Park	Barrier Interior	14	10	4	71	29
Smith Point County Park	Manipulated Dune	10	6	4	60	40
Smith Point County Park	Manipulated Overwash	70	44	26	63	37
Smith Point County Park ^a	New Made Restoration Area	8	2	6	25	75
Smith Point County Park ^a	Great Gun Restoration Area	47	32	15	68	32
Off Site – Bellport to Watch Hill ^c	Backshore	8	4	4	50	50
Total		449	299	150	67	33

^a Not monitored 2013–2014

^b Not monitored in 2013 or 2020

^c Bellport Beach to Watch Hill only monitored 2013–2014

Table 6. Nest fates on the Fire Island and Westhampton Island study area, by year, in each management unit, 2013–2020. Fire Island National Seashore includes nests monitored at Watch Hill from 2013–2014, but Fire Island communities from Kismet to Watch Hill were not monitored following those years. Cupsogue Beach County Park was only monitored 2013–2019.

Year	Management Unit	Total	Successful	Failed			Unknown /Other
				Abandoned	Depredated	Flooded	
2013	Fire Island National Seashore	11	8 (73%)	1 (9%)	-	1 (9%)	1 (9%)
	Smith Point County Park	9	3 (33%)	-	5 (56%)	-	1 (11%)
	Cupsogue Beach County Park	4	3 (75%)	-	-	-	1 (25%)
2014	Fire Island National Seashore	11	4 (36%)	5 (45%)	2 (18%)	-	-
	Smith Point County Park	9	4 (44%)	-	5 (56%)	-	-
	Cupsogue Beach County Park	5	4 (80%)	-	1 (20%)	-	-
2015	Robert Moses State Park	10	5 (50%)	5 (50%)	-	-	-
	Fire Island National Seashore	4	2 (50%)	-	2 (50%)	-	-
	Smith Point County Park	23	2 (9%)	1 (4%)	18 (78%)	-	2 (9%)
	Cupsogue Beach County Park	11	7 (64%)	-	2 (18%)	1 (9%)	1 (9%)
2016	Robert Moses State Park	12	8 (67%)	4 (33%)	-	-	-

	Fire Island National Seashore	9	7 (78%)	1 (11%)	1 (11%)	-	-
	Smith Point County Park	16	12 (75%)	1 (6%)	1 (6%)	-	2 (13%)
	Cupsogue Beach County Park	6	6 (100%)	-	-	-	-
2017	Robert Moses State Park	13	6 (46%)	3 (23%)	-	1 (8%)	3 (23%)
	Fire Island National Seashore	14	10 (71%)	2 (14%)	-	1 (7%)	1 (7%)
	Smith Point County Park	24	19 (79%)	2 (8%)	2 (8%)	-	1 (4%)
	Cupsogue Beach County Park	11	5 (45%)	2 (18%)	2 (18%)	-	2 (18%)
2018	Robert Moses State Park	19	14 (74%)	2 (11%)	1 (5%)	2 (11%)	-
	Fire Island National Seashore	13	10 (77%)	1 (8%)	1 (8%)	1 (8%)	-
	Smith Point County Park	31	20 (65%)	4 (13%)	7 (23%)	-	-
	Cupsogue Beach County Park	7	6 (86%)	1 (14%)	-	-	-
2019	Robert Moses State Park	26	17 (65%)	4 (15%)	2 (8%)	2 (8%)	1 (4%)
	Fire Island National Seashore	29	21 (72%)	3 (10%)	1 (3%)	-	4 (14%)
	Smith Point County Park	37	27 (73%)	6 (22%)	2 (5%)	-	2 (5%)
	Cupsogue Beach County Park	11	7 (64%)	-	2 (17%)	-	2 (17%)
2020	Robert Moses State Park	26	20 (77%)	5 (19%)	-	1 (4%)	-
	Fire Island National Seashore	21	20 (95%)	-	-	-	1 (5%)
	Smith Point County Park	27	22 (82%)	2 (7%)	2 (7%)	-	1 (4%)
Total		449	299 (67%)	55 (12%)	59 (13%)	10 (2%)	26 (6%)

Table 7. Piping plover nest distributions and fates on the Fire Island and Westhampton Island study area, in various habitats of each management unit, April–August 2020. Nest numbers include renests of some pairs. Nests were only designated as within natural overwash if they were within original Hurricane Sandy-created overwashes.

Management Unit	Habitat	Nests			
		Found	Hatched	Failed	Reason for loss
Fire Island National Seashore - east of breach	Natural Overwash	9	9	0	-
Fire Island National Seashore- west of Breach	Natural Overwash	1	1	0	-

Fire Island National Seashore- west of Breach	Backshore	6	5	1	Unknown (1)
Fire Island National Seashore- Lighthouse Tract	Manipulated Dune	3	3	0	-
Fire Island National Seashore- Lighthouse Tract	Backshore	2	2	0	-
Robert Moses State Park	Backshore	17	14	3	Abandoned (2) Flooded (1)
Robert Moses State Park	Dredge Spoil	1	1	0	-
Robert Moses State Park	Barrier Interior	2	2	0	-
Robert Moses State Park	Dune	3	2	1	Abandoned (1)
Robert Moses State Park	Swale	3	1	2	Abandoned (2)
Smith Point County Park	Manipulated Overwash	7	5	2	Depredated (2)
Smith Point County Park	Manipulated Dune	2	2	0	-
Smith Point County Park	Barrier Interior	2	1	1	Abandoned (1)
Smith Point County Park	Backshore	3	3	0	-
Smith Point County Park	Restoration Area	13	11	2	Abandoned (1) Unknown (1)

The number of pairs monitored increased from 19 in 2013 to 86 in 2019 (356.6% increase; Table 8), then decreased to 81 pairs in 2020. However, the study area boundaries have changed throughout the years of monitoring and Cupsogue Beach County Park was not monitored in 2020, bringing the current study area pairs to 71 (Table 9). Across all years of the study, the majority of plovers nested in backshore and overwash habitats. Restoration areas were not created until after the 2014 breeding season, but they were used by piping plovers each season thereafter (Table 8). Using information from USFWS and NPS, we estimated pairs for the entire study area (Robert Moses State Park to Cupsogue Beach County Park) for all six years of the monitoring effort. Though there was fluctuation within management units, the overall number of pairs increased every year following Hurricane Sandy until 2020 (Table 9). In 2020, pair numbers decreased in overwash, breach fill,

restoration, and backshore/barrier interior habitats, but pair distribution across those habitats remained consistent with years past (Table 8).

Table 8. Number of monitored nesting piping plover pairs in each of the various habitats. Restoration areas were not created until after the 2014 nesting season. Some pairs had more than one nest per year, but renests were only counted if the subsequent nest was in a different subsite and habitat class. Table footnotes indicate changes in monitoring area among years.

Habitat	Year							
	2013 ^a	2014 ^a	2015 ^b	2016 ^b	2017 ^b	2018 ^b	2019 ^b	2020^{bc}
Overwash	11	17	15	14	23	21	25	21
Breach Fill	1	1	3	3	3	3	3	2
Restoration	N/A	N/A	5	4	6	10	13	10
Backshore/Barrier Interior	7	3	12	16	13	24	45	38
Total	19	21	35	37	45	58	86	71

^aIncludes Watch Hill nesting pairs, only monitored 2013-2014.

^bIncludes Robert Moses and the Lighthouse Tract only monitored 2015–2020.

^cDoes not include Cupsogue Beach County Park, which was not a part of the study area in 2020.

Table 9. Number of pairs nesting within each management unit. Pair counts for areas not monitored by Virginia Tech in a given year (e.g. Robert Moses State Park in 2013–2014 and all of the study area in 2020) were obtained from USFWS, NPS, New York State Parks, and Suffolk County Parks correspondence and annual reports. These data appear bold and italicized.

Management Unit	Year							
	2013	2014	2015	2016	2017	2018	2019	2020
Robert Moses State Park	<i>12</i>	<i>10</i>	10	9	8	15	22	<i>23</i>
Fire Island Lighthouse	<i>1</i>	<i>1</i>	0	1	1	1	4	<i>5</i>
Fire Island National Seashore West	3	1	1	1	0	1	7	<i>7</i>
Fire Island National Seashore East	4	4	2	6	10	9	13	<i>11</i>
Smith Point County Park	6	8	13	13	20	25	31	<i>25</i>
Cupsogue Beach County Park	3	5	7	6	6	7	9	<i>10</i>
Outside study area - Bellport to Watch Hill	3	3	0	0	0	0	<i>3</i>	<i>1</i>
Outside study area - Davis Park to Kismet	0	0	0	0	<i>1</i>	0	0	<i>5</i>
All Fire Island and Cupsogue	32	32	33	36	46	58	89	<i>87</i>
Total Study Area - Fire Island and Cupsogue	29	29	33	36	45	58	86	<i>81</i>
Total Study Area - Fire Island (no Cupsogue)	26	24	26	30	39	51	77	<i>71</i>

Density

Density in the study area increased from 0.06 pairs/ha of dry sand habitat patches $> 1\text{m}^2$ in 2013 to 0.26 pairs/ha in 2020. Density remained relatively stable from 2013–2017, showed the most increase from 2017–2019, and increased slightly between 2019 and 2020 (Figure 12).

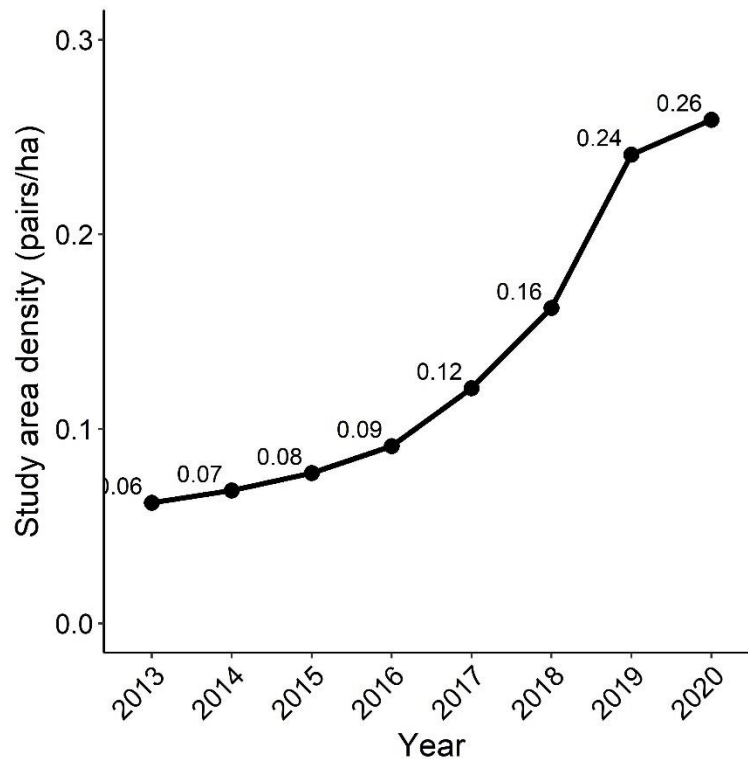


Figure 12. Estimated study area density for each year following Hurricane Sandy. Available habitat was defined as all available dry sand patches greater than 1m^2 using 15-cm classified aerial imagery in each year. For 2013 and 2014, the number of pairs was a combination of the number of pairs monitored by Virginia Tech and the number of pairs estimated at Robert Moses State Park and the Lighthouse Tract. For 2020, the number of pairs was the total estimated by land managers at the National Park Service, New York State Parks, and Suffolk County Parks.

Density increased within all management units during 2013–2019. In 2020, densities in Robert Moses increased, East Wilderness and Smith Point decreased, and West Wilderness and Cupsogue remained stable (Figure 13). Robert Moses State Park density increased from 0.17 to 0.26 pairs/ha between 2019 and 2020. The greatest density was observed at the East Wilderness Area in 2019 (0.42 pairs/ha, Figure 13). For most management units, the lowest density was observed in 2013, directly

following Hurricane Sandy. However, the West Wilderness area did not have any pairs in 2015 or 2017, and therefore density was 0 pairs/ha. The East Wilderness area also had a decline in density between 2014 and 2015, but increased again in 2016 (Figure 13).

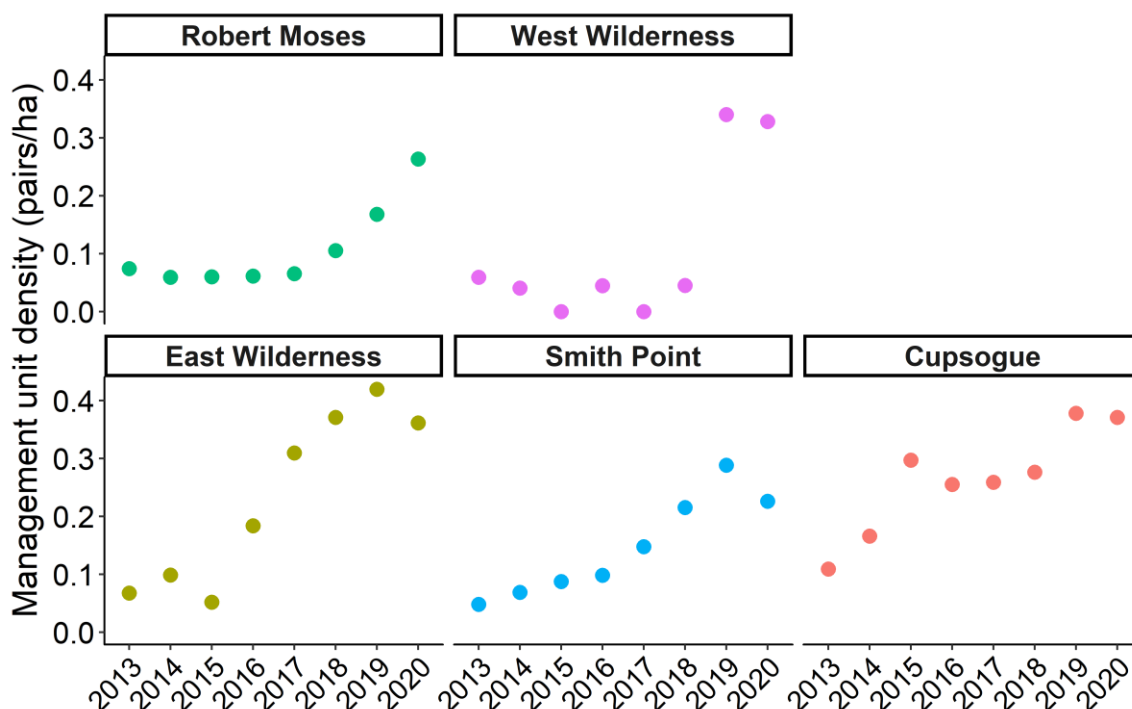


Figure 13. Estimated management unit density for each year following Hurricane Sandy. Available habitat was defined as all available dry sand patches greater than 1m² using 15-cm classified aerial imagery for each year. For 2013 and 2014, the number of pairs was a combination of the number of pairs monitored by Virginia Tech and the number of pairs estimated at Robert Moses State Park and the Lighthouse Tract. For 2020, the number of pairs was the total estimated by land managers at the National Park Service, New York State Parks, and Suffolk County Parks. The Lighthouse Tract was grouped in with Robert Moses State Park for all years.

When we estimated density by subsite, the greatest densities were observed at Old Inlet West in 2019, the small inlet subsite west of Old Inlet (1.17 pairs/ha), Democrat Point in 2020 (0.91 pairs/ha), and Narrow Bay West in 2019 (0.77 pairs/ha). Average subsite density increased from 0.10 in 2013 to 0.37 in 2019 but decreased to 0.28 in 2020 (Figure 14). When separated by subsites with and without bay access, subsites with bay access had, on average, higher densities (Figure 15). During 2013–2019, both subsites with and without bay access increased in density, but the average increase

for bay-accessible sites increased faster as density increased and the thus the difference between the two habitat types widened as density increased. Subsite densities decreased in 2020, yet followed the same trend of higher densities in subsites with bay access (Figure 15).

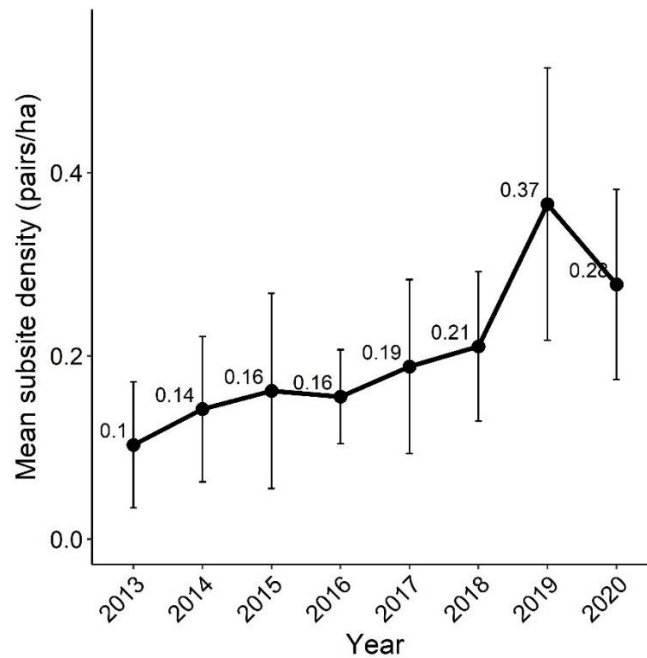


Figure 14. Average subsite density in each year. Subsite extent for density extended the entire width (north to south) of the island. Available habitat was defined as all dry sand patches greater than 1m² using 15-cm classified aerial imagery. Error bars represent 95% confidence intervals.

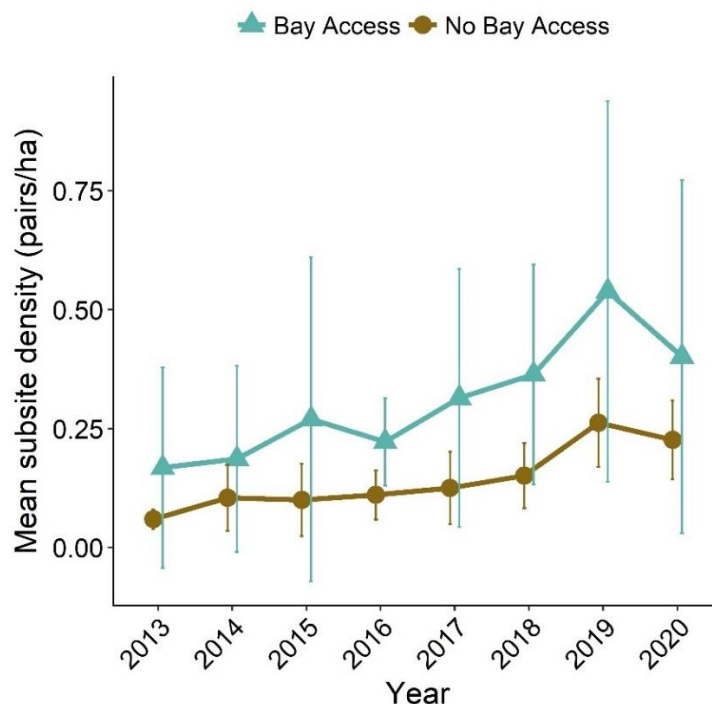


Figure 15. Average subsite density in each year for subsites with bay access (i.e., DMP, OSS/STP, PSO, NBW, CSW) compared to subsites without direct bay access. Subsite extent for density extended the entire width (North to South) of the island. Available habitat was defined as all dry sand patches greater than 1m² using 15-cm classified aerial imagery. Error bars represent 95% confidence intervals.

Discussion

Despite increased habitat and relatively high immigration rates, the population increase in our study area since the hurricane (2013–2019; 186%) was relatively modest compared to some other habitat creating events but is within the range of past observations over similar time periods (42%–745%; Robinson et al. 2019). Less than anticipated growth immediately following Hurricane Sandy may have been related to generally low local and regional reproduction just before and immediately following the storm (USFWS 2019). We estimate that an average of 31% of adult birds die annually (Part 2, Section 5), and there must be enough reproduction to replace those just to maintain a stationary population. Early in the study, the population may have decreased without immigration as it did elsewhere in the NY-NJ recovery unit in 2012–2013. The study area population may have also remained stable following 2014, as immigration was influential to the population increase (Part 2, Section 5, Robinson et al. 2020*b*). During 2013–2019, pairs and nest numbers in our study area

increased, except for a decrease in nests between 2015 and 2016. There were likely more nests in 2015 than 2016 due to the frequency of nest depredation and subsequent renesting. Predators have been known to cue in on nest exclosures and associate them with a food source (Niehaus et al. 2011, Murphy et al. 2003) which, along with the removal of nest exclosures, also may explain why 2015 showed such a high percentage of nest failure compared to other years. In 2020, overall abundance decreased and pairs decreased within all management units except Robert Moses (one pair increase) and the West Wilderness Area (7 pairs consistent with 2019).

Red fox numbers declined across most of our study area, and they were extirpated from some sites during 2015–2019 due to a natural outbreak of sarcoptic mange. No foxes were detected from April 2016 to March 2017 east of Old Inlet, including Smith Point County Park, and only one was believed to inhabit that area intermittently during 2017–2018 (Part 3, Section 2). In the years following this fox decline, plover nests experienced lower depredation rates. Nest abandonment was the greatest reason for nest failure in every year after 2015, except 2018, when at least one red fox was present at Smith Point County Park. Population growth rate in the study area began to increase following the extirpation of foxes, and thus it is likely that red fox predation, to some degree, was limiting population growth on the Fire Island portion of the study area.

Plover pairs nested in natural and manipulated overwash habitats the most from 2013–2019 but by 2020, backshore and barrier interior habitats became the most used of all habitat types. From 2013–2018, pairs nested in backshore and barrier interior habitats nearly as often as overwash and, when compared to what was available, avoided backshore and barrier interior habitats (Part 2, Section 5). However, backshore and interior habitats were used more often in 2019 and 2020. An important habitat distinction of note is the difference between Hurricane Sandy-created overwashes and overwashes created by other storm events. Since 2012, there have been multiple occasions where a storm surge created overwash habitat on a smaller scale than Hurricane Sandy. For example, in 2019, we observed new overwash habitat west of Old Inlet on Fire Island National Seashore. Following this overwash, Old Inlet West pair numbers increased 7-fold, from one pair in 2018 to seven in both 2019

and 2020. While technically overwash habitat, many of the nests in newly-created overwashes were classified as "Backshore/Barrier Interior" since they were not a result of Hurricane Sandy, and our objective was primarily to understand the effect of Hurricane Sandy on the plover population. Though created at different times, these overwashes are fundamentally the same as the Hurricane Sandy natural overwash and as a result, our estimates on plover usage of overwash habitats are lower than in reality.

We found that pair density nearly quadrupled from 2013, the first breeding season following Hurricane Sandy, to 2020. A decrease in pair abundance between 2019 and 2020 coupled with a decrease in available dry sand nesting habitat resulted in only a 0.02 increase in density between the two years. Much of the trend in overall study area density was driven by Smith Point and Robert Moses, as these sites were greater than twice the area of the other management units. Interestingly, the two sites saw contrasting density trends in 2020. Robert Moses consistently increased in density each year, despite only a two pair increase between the 2019 and 2020 breeding seasons. This is likely due to limited dry sand nesting habitat at Democrat Point at the time our imagery was collected in 2020, which lowered the classified dry sand habitat and thus continued to increase density at that site. We suspect that densities at Smith Point lowered slightly from 0.29 pairs/ha in 2019 to 0.23 pairs/ha in 2020 due to some vegetation removal at Great Gun in 2020. The West Wilderness Area and Cupsogue did not exhibit changes in density between 2019 and 2020 due to a stabilized pair count (West Wilderness) and slight decrease (Cupsogue) and little change in available dry sand habitat between the years.

We originally hypothesized that density should begin to decline as the piping plover population on Fire Island reached carrying capacity. In a study of Westhampton Island, Cohen et al. (2009) identified carrying capacity to be 1.05 pairs/ha in two-sided habitats (ocean-side and bay-side connected by sand traversable by a walking plover) and 0.50 in one-sided habitat (no sand connection between ocean and bay), and this was the point at which the population began to decline. Remarkably, the density within this study in 2020, eight years after Hurricane Sandy, is only about a

quarter of what Cohen and coauthors found for two-sided habitats and half that found in one-sided habitat. However, density, like many population parameters, is highly sensitive to the boundaries in which it is defined. Here we classified available piping plover nesting habitat as any patch of dry sand at least 1-m² composed of 15-cm dry sand pixels. This fine-scale habitat delineation likely identified patches of habitat as available that would be excluded with a coarser level of habitat identification, making cross-study comparison challenging. In 2020, pair numbers decreased for the first time since Hurricane Sandy. However, after eight years of plover monitoring following Hurricane Sandy, reproductive output has not yet declined below what would be needed for stationarity (Weithman et al. 2019) nor has immigration slowed considerably (Part 2, Section 5). Therefore, it appears that this population may be reaching carrying capacity. Continued monitoring of plovers and their predators following the 2020 breeding season is crucial to understand carrying capacity and what population size and density is sustainable on Fire and Westhampton Islands in the presence of a recovering, post-mange red fox population.

Given this population's high reproductive output, the number of immigrants and vegetative succession, nesting habitat may soon limit the population. After Hurricane Sandy, vegetation increased in each of the newly created habitats from 2013–2017, especially in overwash areas (Bellman 2018), where it exceeded the 30% vegetation cover threshold established under the BO (U.S. Fish and Wildlife Service 2014). From 2018–2020, we continued to see vegetation encroach on dry, sandy areas across our study area. This increase in vegetation is happening concurrently with overall increases in plover density. Piping plovers generally nest in sparsely vegetated or flat, open sand due to the potential increased risk of depredation associated with dense vegetation (Espie et al. 1996, Cohen 2008). Cohen et al. (2009) observed that the piping plover population declined at their study area (West Hampton Dunes, NY) as nesting habitat degraded due to vegetation growth. An earlier study by Wilcox (1959) also cited increasing vegetation density as a possible reason for plovers deserting a study area east of Moriches Inlet. Therefore, we expect that suitable nesting habitats will

continue to decline with vegetation succession and thereby influence population growth within our study area.

In the early spring of 2019, a large portion of vegetation at the Great Gun restoration area was removed mechanically, resulting in a 4.06 ha expanse of sand nearly devoid of vegetation. In March 2020, mechanical devegetation occurred in Great Gun restoration area. Continued vegetation management may be required to maintain open patches of preferred nesting habitat in areas of dramatic vegetation encroachment or in sites where vegetation inhibits chick access to foraging habitat.

During 2013–2019, we banded 1,006 piping plovers on Fire and Westhampton islands. As a result, we were able to uniquely identify individuals and accurately track population change through the years. These data are crucial for determining site fidelity and survival for plovers. Unfortunately, we were unable to band any piping plovers in 2020, which will cause limitations in future years of data analysis and interpretation. However, in future years we intend to resume our banding effort. Banding individual plovers has led to valuable insight regarding many facets of plover population dynamics that can ultimately have an influence on management decisions for the species. Without such an effort, it would have been difficult or impossible to determine the implications of Hurricane Sandy on the plover population within our study area and the mechanisms of any population change.

The implications of this study on plover population dynamics are numerous, but further investigation is required to understand the factors influencing this population's growth and eventual limitations. Although carrying capacity has not been met, with the drastic decrease in number of red foxes on Fire Island, there is one less factor potentially working against vital rates in this population. Indeed, the local predator community has played an important role on reproductive output (Part 2, Section 4) and the population growth rate, but we also have observed greater conspecific disturbance and competition each year as density increases. Further, the red fox population is expected to rebound from mange-related mortalities in the coming years. The succession of plant communities at a natural rate and accelerated by anthropogenic activities like dune construction and snow fence

installation also has been occurring in the overwashes and breach fill habitats for over eight years and is contributing to nesting and foraging habitat loss and fragmentation. Without the creation of new habitat, either mechanically or naturally, this population may soon begin to experience negative density dependent feedback as habitat availability decreases (Cohen et al. 2009). How the population responds to these pressures within the following few years will be crucial in determining carrying capacity in our study area and the limitations that define it.

Section 4: Compare piping plover nest and chick survival rates in various habitats across Fire Island

Introduction

Reproductive output has been shown to correlate with population change in piping plovers (Saunders et al. 2018). For Atlantic piping plovers, nest survival tends to be high due to the installation of nest exclosures (Melvin et al. 1992). Nest exclosures, however, do not prevent all causes of nest failure, such as flooding or predation by predators that can fit inside nesting exclosures (e.g., ghost crabs (*Ocypode quadrata*; Kwon et al. 2018) or American mink (*Neovision vision*; M. Stantial, personal communication)). Once precocial chicks have hatched, the nest exclosure is no longer useful at protecting the chicks, which move about and forage for themselves soon after hatch. Therefore, it is important for the next generation of plover management and conservation to better understand the best methods to improve plover chick survival and reproductive output given the challenges of plover management outside of their breeding areas. Plover chick survival could be influenced by habitat suitability and could be reduced if chicks need to move around a lot to avoid predators or access suitable foraging habitat. Thus, understanding the suitability of habitat and movement and home range size of broods could inform future management to increase survival of piping plover chicks.

Fire Island reproductive output has been assessed in terms of human disturbance (DeRose-Wilson et al. 2018) and in comparison to a more southerly site (Weithman et al. 2019). We also were interested in any relationship between reproductive output time since Hurricane Sandy, and geomorphic and habitat variables. Specifically, we were interested in effects of artificially-created nesting habitats for piping plovers, which were built intentionally (restoration areas), built for island stabilization (breach fills), and were created by the hurricane (natural and manipulated overwash; Table 2). Home range size and movement of broods also may vary by habitat types, and may further contribute to reproductive output dynamics through effects on growth and survival in some species (Lengyel 2006, Nichols and Kaiser 1999). If it is determined that a specific habitat feature, natural or

artificial, can positively influence reproductive output and thus influence the overall population in the study area, perhaps future habitat management can try to replicate those features.

Here, we focused on the components of reproductive output (nest survival, chick survival) and some potential drivers of chick survival (i.e., movement and home range) on Fire and Westhampton Island following Hurricane Sandy and the FIMI project. Our objectives were to understand 1) the influence of red fox (*Vulpes vulpes*), raccoon (*Procyon lotor*), and feral cat (*Felis catus*) abundance on piping plover chick survival, 2) how movement and home range size change in relation to habitat and time since Hurricane Sandy, and 3) which of these factors had the greatest influence on piping plover nest and chick survival.

Methods

Nest Survival

We used a logistic exposure model (Rotella et al. 2004, Shaffer 2004) to estimate the daily survival rates of piping plover nests from 2013–2019. We built models that compared survival between exclosed and unexclosed nests (i.e., large, wire cages placed around nests to reduce predation; Melvin et al. 1992), management units, and habitat types [breach fill, manipulated overwash, natural overwash, restoration, other]. All categorical habitat variables were analyzed in reference to the 'other' habitat type, to understand how nest survival in newly created habitats compares to pre-Hurricane Sandy habitats. A nest was considered exclosed only during the period when the exclosure was present. When predicting from this model, hatch date was set at 34 days from initiation date (Heisey et al. 2007).

To distinguish whether nest survival was affected by predator abundance, habitat, density, or weather, we developed a full model, which estimated the effect of continuous variables on nest survival. We used nest initiation date, nest age, nesting plover density, maximum temperature, average wind speed, total precipitation, distance to vegetation and elevation, and least cost distance to ocean and bay. We also included a random effect of subsite and year. Using this same model, we

subset our nests by the areas in which predators were monitored (i.e., not Cupsogue), and included a categorical effect of pre- and during- the mange outbreak in comparison to post-mange outbreak (Part 2, Section 1; Pre-mange was 2013–2015 East of Old Inlet and 2013–2017 West of Old Inlet; post-mange was 2016–2019 east of Old Inlet, 2018–2019 west of Old Inlet). Cupsogue was removed because we did not have knowledge of the predator community nor mange at Cupsogue. In order to focus more carefully on predator numbers, we built a second model, only including the years of the concurrent fox study (Part 2, Section 1), 2015–2018, and only including management units where foxes were monitored. This model included all of the previously mentioned variables, but instead of a categorical fox variable, we included trap success (# detections/100 trap nights; Part 2, Section 1) of red fox, feral cat (*Felis catus*) and raccoon (*Procyon lotor*).

Chick 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. We considered several models to derive estimates of chick survival for the whole study area. These included an annual survival model, one which estimated chick survival among management units, and another that estimated chick survival among habitat types [breach fill, manipulated overwash, natural overwash, restoration, other]. All categorical habitat variables were in reference to the 'other' habitat type, which was any habitat that did not fall into the other four but was primarily backshore habitats that existed prior to Hurricane Sandy, to understand how newly created habitats compare to pre-Sandy habitats. To estimate the study, habitat, and management-unit-specific probability of survival to fledge, we calculated the product of the five 5-day interval survival rates from the year-specific model.

As we did for nest survival, we developed two full models to understand whether chick survival was affected by habitat, weather, density, or time. In comparison to the nest survival model, we were

limited by the number of covariates we could include due to small sample size and model complexity. We included a linear trend of time, hatch day, maximum temperature within the 5-day interval, average wind speed over the 5-day interval, average least cost distance to ocean, least cost distance to bay, distance to development and distance to vegetation over each 5-day interval, and management-unit nesting plover density. Distance variables were calculated as average distance variables within 5-meters of chick use points, and were averaged over the 5-day interval prior to detection. We developed a separate model without Cupsogue, because no predator information was known from Cupsogue. We included the categorical variable of pre- and during mange as compared to post mange, as described above for nest survival. We also developed a model of chick survival using trap success of red fox, raccoon, and feral cats and nesting density as dependent variables using data from 2015–2018, the years the plover and fox projects were concurrent. Plover density and predator trap success were measured at a management-unit level.

Because we used models in a Bayesian framework, we evaluated the influence of explanatory variables using both the overlap of the 95% credible interval with 0 and the proportion of the posterior distribution that has the same sign as the mean effect (Catlin et al. 2019*b*).

Reproductive Output

We estimated reproductive output using annual monitored pair counts and the number of fledglings observed for each year. Chicks were considered fledged if they reached 25 days of age or were observed in sustained flight. Using nesting plover density estimates (Part 2, Section 3), we tested for the correlation between reproductive output and subsite nesting density, management unit nesting density, and study area nesting density (Fire Island to Cupsogue), using Pearson's correlation coefficient, to determine if we could detect a relationship between reproductive output and density.

Finally, we compared piping plover productivity before and after the mange outbreak. For one management unit (Cupsogue), the predator community was unknown, and was considered separately. Fledglings produced per pair were calculated for specific management units, with the Lighthouse

Tract grouped into Robert Moses State Park and the Fire Island Wilderness split into areas East and West of Old Inlet.

Brood Home Range

We created minimum convex polygons (MCP) as brood home ranges from 2014–2019 using the “adehabitatHR” package in Program R (Calenge 2006, R Version 3.3.1). We only calculated home range size for broods that had ≥ 5 location points available. We first estimated cumulative home range size as the age of the brood increased to understand how age affected home range size. We then subset the home ranges from broods that fledged at least one chick, to control for broods that had fewer points and smaller home ranges due to early chick mortality. We used a Kruskal-Wallis to test whether there was difference between area of brood home range and habitat type [breach fill, manipulated overwash, natural overwash, restoration, other], and we used linear regression to test for a difference between broods with bay access or not, controlling for the number of points used in the estimate of the MCP.

We developed a full model, which tested whether home range size varied by year, habitat type, distance to vegetation, development, least cost distance to bay and ocean, and management unit nesting density. Distance variables were measured from the brood home range centroid. Finally, to understand whether the red fox mange outbreak had an effect on home range size, we developed a model with only Fire Island broods (i.e., excluding Cupsogue) and included a post-mange variable. In all models, we also included the number of points used to estimate the home range, and log transformed brood home range size to normalize the response variable.

Brood Movement

We calculated the movement of broods between successive daily observations (time between observations = 1 day). If we collected more than one brood location in a day, we selected the last location collected in a day (Weithman 2019). If we first observed the brood outside of the nest bowl,

we added in a location at the nest site on the hatch day. We then used the “geosphere” package in Program R to calculate the Euclidean distance from every point to the one preceding it (Hijmans 2016), and scaled locations by the time between observations, removing observations that the time between observations was greater than 1 day. We used a Wilcoxon Rank Sum test to assess whether there was a difference in daily movement rates for broods with or without direct bay access, and used a Kruskal-Wallis test whether there was difference between area of brood home range and accessible foraging habitats (breach fill, restoration, natural overwash, manipulated overwash, and other).

Results

Nest Survival

The probability of surviving to hatch varied across years from 2013–2019 (Table 10). Nest survival was highest in 2016 and lowest in 2015. Overall, nests that were exclosed during or after clutch completion had a higher predicted probability of surviving to hatch than unexclosed nests (Figure 16). Survival to hatch for exclosed nests ranged from 0.51–0.84, and survival to hatch for unexclosed nests ranged from 0.22–0.67 (Figure 16). However, in 2015, midway through the nesting season, exclosures were removed from all of the Smith Point County Parks nests (approximately 15 days after clutch completion) due to a high incidence of fox harassment at exclosed nests. The nests in 2015 that were “previously exclosed” had a 0% probability of surviving to hatching (Monk et al. 2015).

Table 10. Predicted probability of plover nests surviving to hatch (34 days from initiation) for all four management units in 2013–2019. The predicted probability comes from a logistic exposure model, estimating the interactive effect of year and management unit on daily survival, and then raised to the 33rd power.

Management Unit	Year	N Nests	Survival Estimate	Lower 95% CI	Upper 95% CI
Fire Island National Seashore	2013	7	0.67	0.29	0.95
Smith Point County Park	2013	9	0.27	0.06	0.59
Cupsogue County Park	2013	4	0.70	0.20	0.99
Fire Island National Seashore	2014	6	0.51	0.17	0.86
Smith Point County Park	2014	9	0.50	0.22	0.79
Cupsogue County Park	2014	5	0.78	0.36	0.99
Robert Moses	2015	10	0.63	0.35	0.88
Fire Island National Seashore	2015	4	0.57	0.16	0.92
Smith Point County Park	2015	23	0.12	0.04	0.25
Cupsogue County Park	2015	11	0.59	0.29	0.86
Robert Moses	2016	11	0.70	0.40	0.92
Fire Island National Seashore	2016	9	0.77	0.46	0.97
Smith Point County Park	2016	14	0.84	0.60	0.98
Cupsogue County Park	2016	6	1.00	0.95	1.00
Robert Moses	2017	12	0.45	0.19	0.73
Fire Island National Seashore	2017	14	0.71	0.45	0.91
Smith Point County Park	2017	24	0.77	0.58	0.92
Cupsogue County Park	2017	11	0.36	0.12	0.67
Robert Moses	2018	19	0.71	0.48	0.89
Fire Island National Seashore	2018	13	0.75	0.49	0.94
Smith Point County Park	2018	29	0.65	0.47	0.82
Cupsogue County Park	2018	7	0.86	0.54	1.00

Robert Moses	2019	25	0.66	0.46	0.83
Fire Island National Seashore	2019	29	0.68	0.49	0.84
Smith Point County Park	2019	35	0.73	0.56	0.87
Cupsogue County Park	2019	12	0.56	0.26	0.84

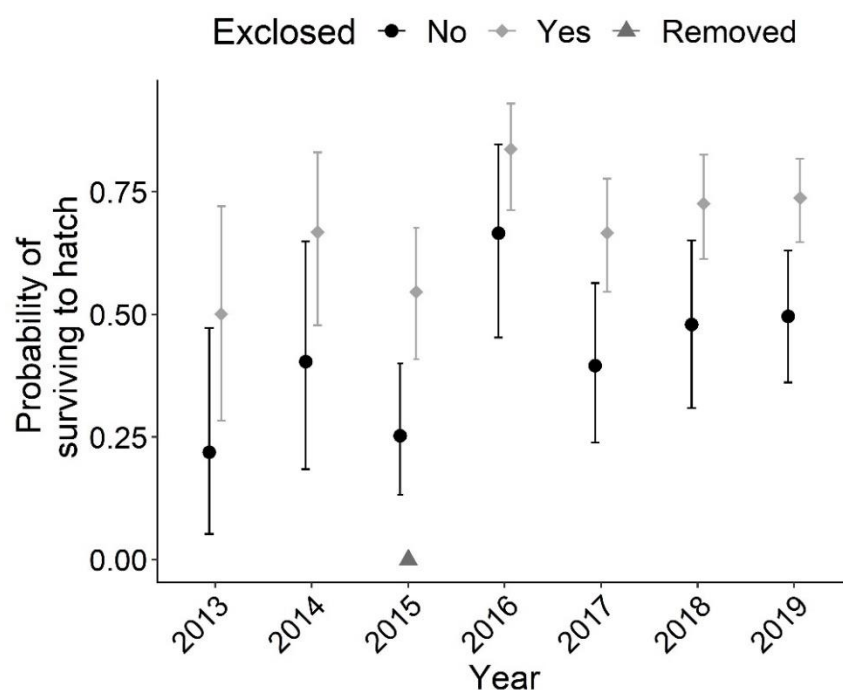


Figure 16. The probability of piping plover nests surviving to hatching with an exclosure and without an exclosure on Fire Island and Westhampton Island, 2013–2019. Error bars represent 95% credible intervals.

When comparing nest survival among the five habitat types [breach fill, manipulated overwash, natural overwash, restoration area, and other], nest survival was not significantly affected by habitat. The mean effect indicated lower nest survival for restoration areas, breach fills and manipulated overwash compared to 'other' habitats, but 95% credible intervals overlapped zero for all habitat types (see Robertson et al. 2019 for supplementary materials).

Of all variables examined “exclosed” had the greatest positive relationship with nest survival (Figure 17). Nesting plover density, temperature, and the number of eggs in a nest also correlated positively with nest survival, whereas nest age and wind had negative relationships with nest survival (Figure 17). When we added the categorical fox effect into the model (pre/during vs. post mange), nest survival was higher in the post-mange years than in the years prior to and during the mange outbreak (Figure 17). The relationship between nest survival and nesting plover density switched signs, resulting in a negative relationship, although not significant. Finally, from the model assessing fox, feral cat, and raccoon trap success during 2015–2018, trap success of red fox, feral cat and raccoon from the winter camera grid did not explain variation in nest survival, but plover nesting density was positively related to nest survival (Figure 18).

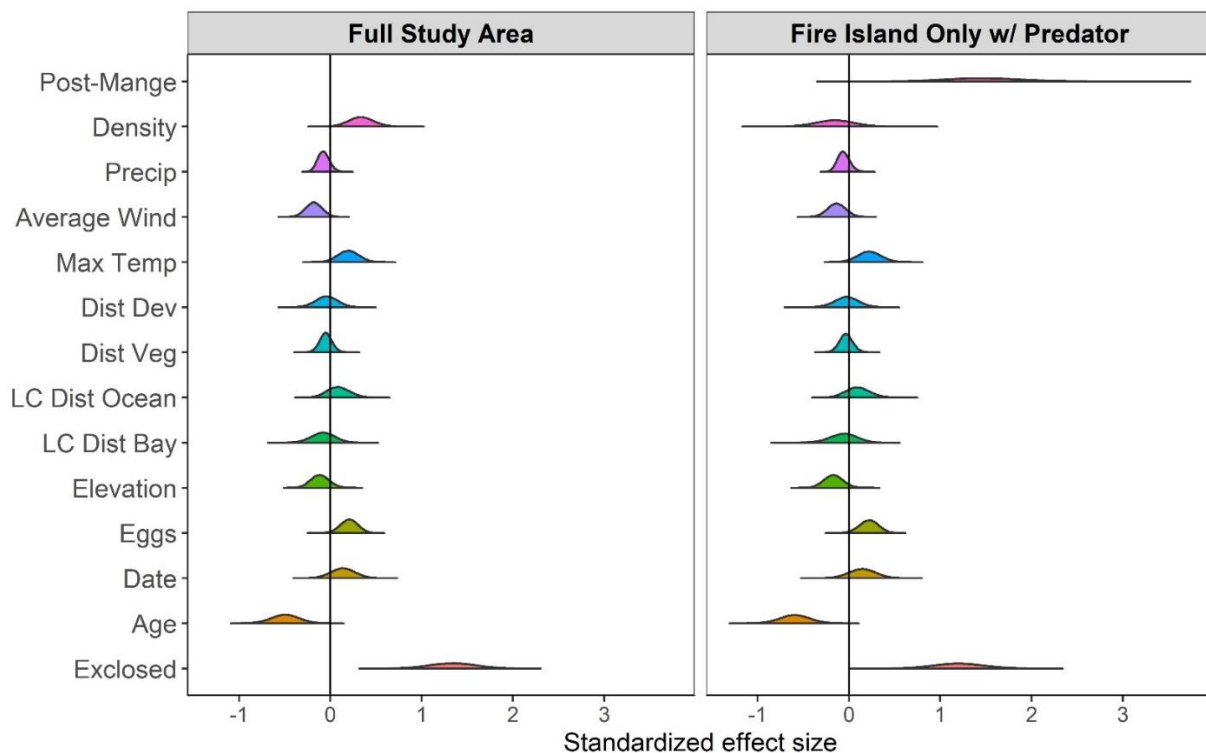


Figure 17. Posterior distribution of nest survival coefficients from a logistic exposure model testing the effects of management-unit and interval specific variables on nest survival. Model was developed using all data, 2013–2019 (left) and only Fire Island management units for the same years but including the effect on nest survival of pre- and during the sarcoptic mange outbreak on the red fox population, as compared to post-mange (right).

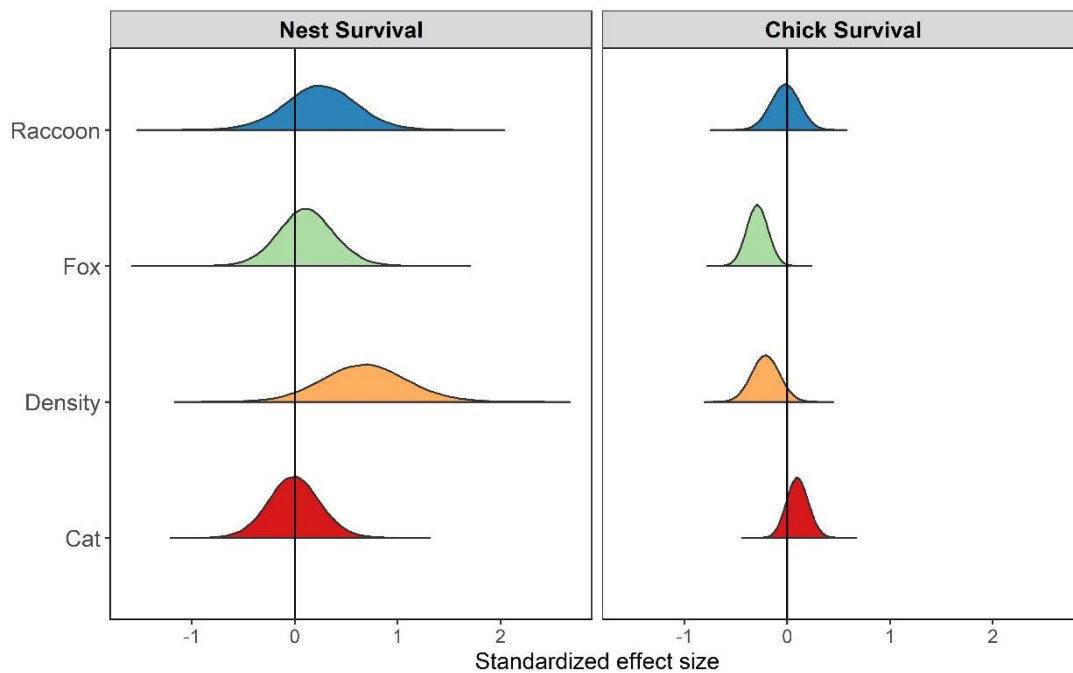


Figure 18. Posterior distribution of standardized nest and chick survival coefficients illustrating the effect of raccoon trap success, red fox trap success, nesting plover density and feral cat trap success on chick survival, on Fire Island during 2015–2018. Nest survival coefficients resulted from a logistic exposure model, and chick survival coefficients resulted from a modified Dail-Madsen chick survival model. Trap success was estimated at the management unit level as # species detections/100 trap nights from concurrent predator monitoring at game camera grids occurring from Robert Moses State Park to Smith Point County Park.

From 2013–2020, 47 of 430 nests were abandoned (11%, Table 11). From the 47 abandoned nests, 12 nests belonged to a pair of unbanded or unknown adults, 15 nests belonged to a pair with one banded adult, and 20 nests belonged to a pair of banded adults. Of the 20 nests with a pair of banded adults, all but one nest (95%) had at least one individual resighted after the nest was abandoned. There were two nests (10%) where both banded individuals were seen after abandonment. Of the 15 nests with one banded adult, nine banded individuals (60%) were seen after nest abandonment. In 2020, two banded individuals from nests with one banded adult were not seen again, although search effort of banded birds in 2020 was not consistent with that of years prior. Of 55 banded birds from 47 abandoned nests, 30 banded individuals (55%) were seen after their nest was abandoned. Only 11 of those 30 banded individuals renested within the same season.

Throughout the duration of this study, we recorded four occasions in which a nest was abandoned around the same time as the mortality of one of the incubating adults. We discovered the remains of three of these banded adults within 90 meters of their nest exclosures.

Table 11. Abandonment rate of piping plover nests with exclosures and without exclosures on Fire Island and Westhampton Island study area 2013–2020.

Year	Exclosed	# of Nests	Failed	Hatched	Abandoned	Abandonment ^a Rate
2013	N	6	5	1	0	0.00
2013	Y	14	4	10	1	0.07
2014	N	8	5	3	0	0.00
2014	Y	12	4	8	2	0.17
2015	N	25	20	5	2	0.08
2015	Y	23	12	11	5	0.22
2016	N	8	3	5	1	0.13
2016	Y	32	4	28	4	0.13
2017	N	16	14	2	4	0.25
2017	Y	45	7	38	4	0.09
2018	N	9	9	0	1	0.11
2018	Y	58	8	50	6	0.10
2019	N	22	15	7	1	0.05
2019	Y	78	13	65	9	0.12
2020	N	25	7	18	3	0.12
2020	Y	49	5	44	4	0.08
2015	Removed	5	5	0	0	0.00
All	N	119	78	41	12	0.10
All	Y	311	57	254	35	0.11

^a Calculated as the # of abandoned nests/total nests

Chick Survival

From 2013 to 2019, we monitored 233 broods. Sixty-seven additional broods were monitored by land managers in 2020 but were not all regularly observed, therefore, were not used for this analysis. Chick survival to fledge was highly variable among years, with the lowest survival rate in the first year of the study, 2013, and the highest rate in 2018 (Figure 19, Table 12). Relative to other habitats, chicks hatching in a manipulated or a natural overwash relative to other habitats had a positive effect on chick survival. Hatching in a breach fill had a negative effect on chick survival, and hatching in a restoration area had no detectable effect on chick survival (Robertson et al. 2019).

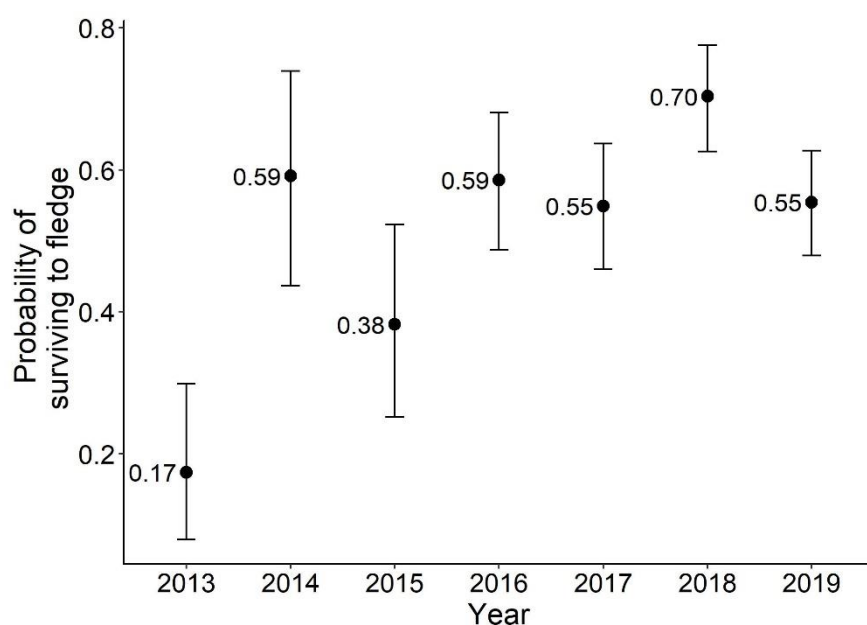


Figure 19. Probability of surviving to fledge (25 days) for chicks 2013–2019 on Fire Island and Cupsogue Beach County Park. Error bars represent 95% credible intervals.

Based on the full chick survival model (i.e. including Cupsogue), broods 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 that were farther from the ocean and the bay during a 5-day detection window had higher survival. Nesting plover density also was negatively with chick survival (Figure 20). When we removed Cupsogue from the model (resulting N = 195), chick survival was greater during the post-mange period, although only 90% of the posterior

distribution agreed with the sign of the mean effect (Figure 20). Without Cupsogue broods, least cost distance to ocean and bay variables were no longer correlated with chick survival, however distance to development became important, suggesting that broods that were farther from development (i.e. paved roads, parking lots, buildings) had lower survival (Figure 20). When we included the categorical effect of post-mange on chick survival, chick survival was greater during the post-mange period.

Table 12. Probability of surviving to fledge for chicks in all management units 2013–2019, estimated from a young survival model. Probability of surviving to fledge represents the probability of surviving to 25 days old.

Management Unit	Year	N Broods	Survival to fledge	Lower 95% CI	Upper 95% CI
Robert Moses	2015	5	0.54	0.29	0.78
	2016	8	0.41	0.23	0.60
	2017	6	0.84	0.65	0.97
	2018	14	0.73	0.59	0.85
	2019	17	0.62	0.49	0.74
Fire Island National Seashore	2013	5	0.16	0.05	0.34
	2014	3	0.55	0.26	0.84
	2015	2	0.99	0.87	1.00
	2016	7	0.75	0.55	0.91
	2017	10	0.48	0.32	0.64
	2018	10	0.73	0.57	0.86
	2019	21	0.74	0.61	0.85
Smith Point County Park	2013	3	0.36	0.10	0.67
	2014	4	0.80	0.58	0.96
	2015	2	0.56	0.21	0.88
	2016	12	0.79	0.64	0.90
	2017	19	0.54	0.41	0.67

	2018	20	0.70	0.57	0.81
	2019	27	0.50	0.39	0.61
	2013	3	0.10	0.01	0.30
	2014	4	0.44	0.22	0.68
	2015	7	0.12	0.03	0.28
Cupsogue County Park	2016	6	0.29	0.12	0.50
	2017	5	0.45	0.22	0.70
	2018	6	0.68	0.45	0.89
	2019	8	0.30	0.16	0.47

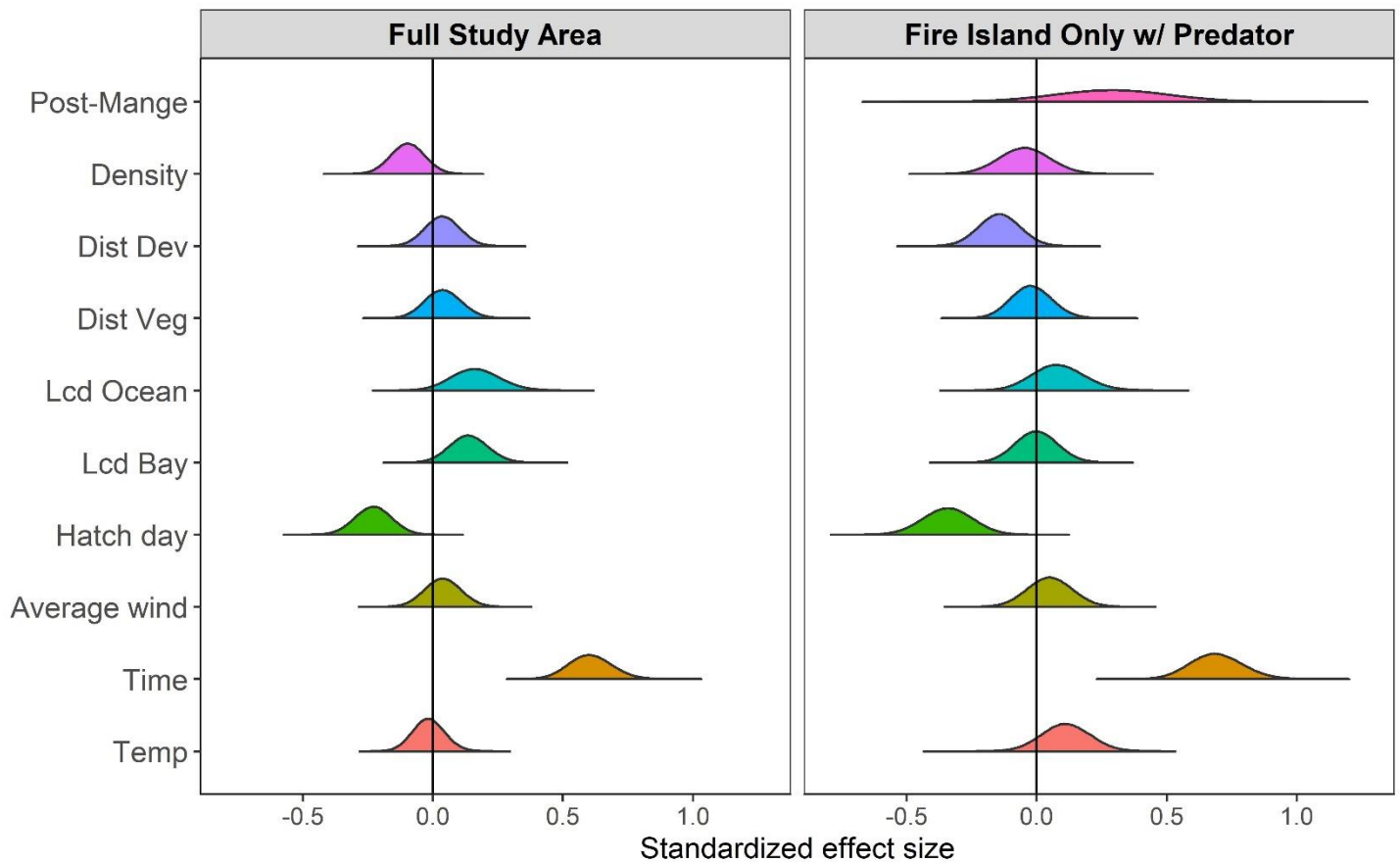


Figure 20. Standardized model coefficients from a chick survival model with the full study area (i.e., Robert Moses to Cupsogue, left) and Fire Island only (i.e., no Cupsogue) but including the effect on chick survival of pre- and during the sarcoptic mange outbreak on the red fox population, as compared to post-mange (right). Model estimates are from a modified Dail-Madsen model implemented in a Bayesian framework.

Red fox trap success, followed by piping plover nesting density, best described chick survival in the 2015–2018 subset model (Figure 18). Higher plover nesting density and higher red fox trap success were correlated with lower chick survival, and that raccoon and feral cat trap success did not have an effect on chick survival (Figure 18).

Reproductive Output

Piping plover reproductive output across the study area was variable among years, with the highest study area reproductive output (2.02 fledglings/pair) in 2018 and the lowest observed

reproductive output (0.39 fledglings/pair) in 2015 (Table 13). Reproductive output was not correlated with subsite density ($r = 0.067$, $P = 0.48$), management unit density ($r = 0.25$, $P = 0.12$), or annual study area density ($r = 0.60$, $P = 0.12$). There was some evidence that reproductive output was related to the mange outbreak that occurred in 2015 on the eastern side of Old Inlet and in 2018 on the western side of Old Inlet. However, not all variation in reproductive output can be attributed to a change in predator dynamics, as some high years of reproductive output occurred prior to the mange outbreak (Figure 21).

Table 13. Piping plover pair counts and productivity (fledglings/pair; Ro) in four different management units on Fire Island and Westhampton Island, 2013–2020. Pairs is the number in each subsite, and Ro is the reproductive output (chicks fledged/pair).

Year		Robert Moses State Park	Fire Island National Seashore ^a	Smith Point County Park	Cupsogue Beach County Park	Total
2013	Pairs	-	10	6	3	19
	Ro	-	0.6	0.5	0	0.47
2014	Pairs	-	8	8	5	21
	Ro	-	0.75	1.5	1.2	1.14
2015	Pairs	10	3	13	7	33
	Ro	0.3	1.67	0.31	0.14	0.39
2016	Pairs	9	8	13	6	36
	Ro	1.11	2	2.38	1	1.75
2017	Pairs	8	11	20	6	45
	Ro	1.75	1.64	1.7	0.67	1.56
2018	Pairs	15	11	25	7	58
	Ro	2.27	2.64	1.8	1.29	2.02
2019	Pairs	22	24	31	9	86
	Ro	1.36	1.83	1.32	1	1.44
2020	Pairs	23	23	25	10	81
	Ro	1.65	2.22	2.08	1.10	1.75

^a Does not include outside the study area (Bellport to Kismet)

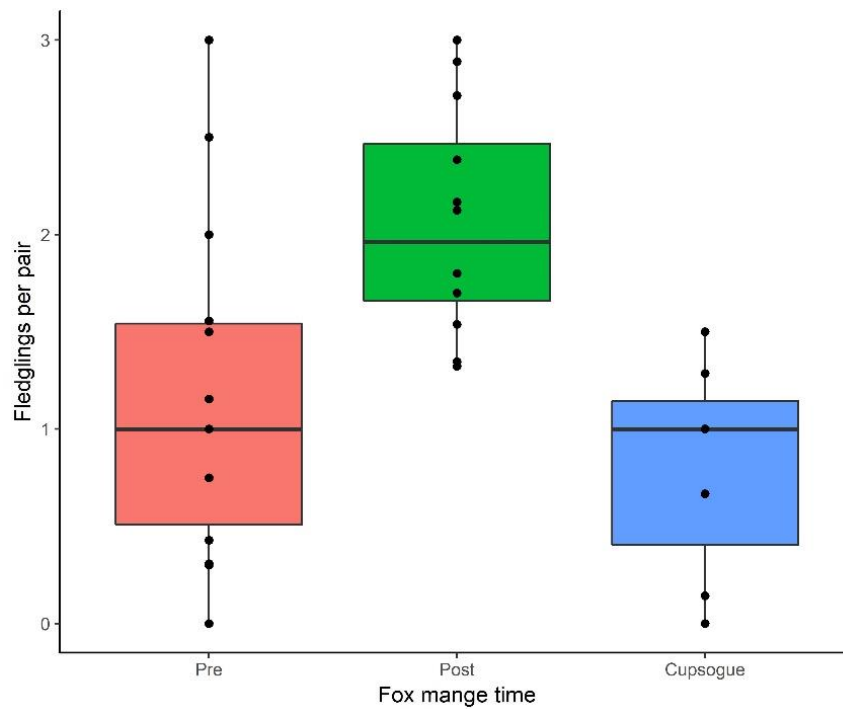


Figure 21. Fledglings per pair in relation to known mange outbreaks in the red fox population on Fire Island. Pre-mange outbreak includes 2013–2015 east of Old Inlet and 2013–2017 west of Old Inlet. Post-mange outbreak is all other dates excluding 2020. Cupsogue is separate, as fox monitoring does not occur at Cupsogue County Park, and few foxes or tracks have been observed. Data points for fledglings per pair are productivity for specific management units, with the Lighthouse Tract grouped into Robert Moses State Park, and the Fire Island Wilderness split into areas East and West of Old Inlet. Boxplots in this figure illustrate the median as the central horizontal line within the box and the first and third quartile as the extents of the colored box. The maximum and minimum are illustrated by lines extending out from the interquartile range. Points overlaying the plots illustrate observed reproductive output data points.

Brood Home Range

Cumulative brood home range size increased as broods aged (Figure 22); therefore, to account for potential mortality of broods, and thus smaller home ranges, we continued analyses with only broods that fledged at least one chick. Broods that fledged at least one chick ($N = 169$) with direct access to bayside foraging habitat in their nesting subsite (STP, PSO, NBW, CSW and DMP) had smaller home ranges ($\bar{x} = 2.92$ ha, $SE = 0.26$) than broods that did not have such access ($\bar{x} = 4.74$ ha,

SE =0.55; Figure 23). While the relative difference was similar in 2019, the differences were not significant (K-W $\chi^2=4.89$, $P=0.30$, Figure 23, Table 14).

Home ranges of broods that fledged at least one chick did not differ among years, but restoration area broods had larger home ranges. When we removed Cupsogue broods and added in the pre- and during as compared to post-mange outbreak variable, home ranges were smaller in 2019, and manipulated overwash broods had smaller home ranges (Robertson et al. 2019). Home range size of plover broods did not correlate with the timing of the fox mange outbreak.

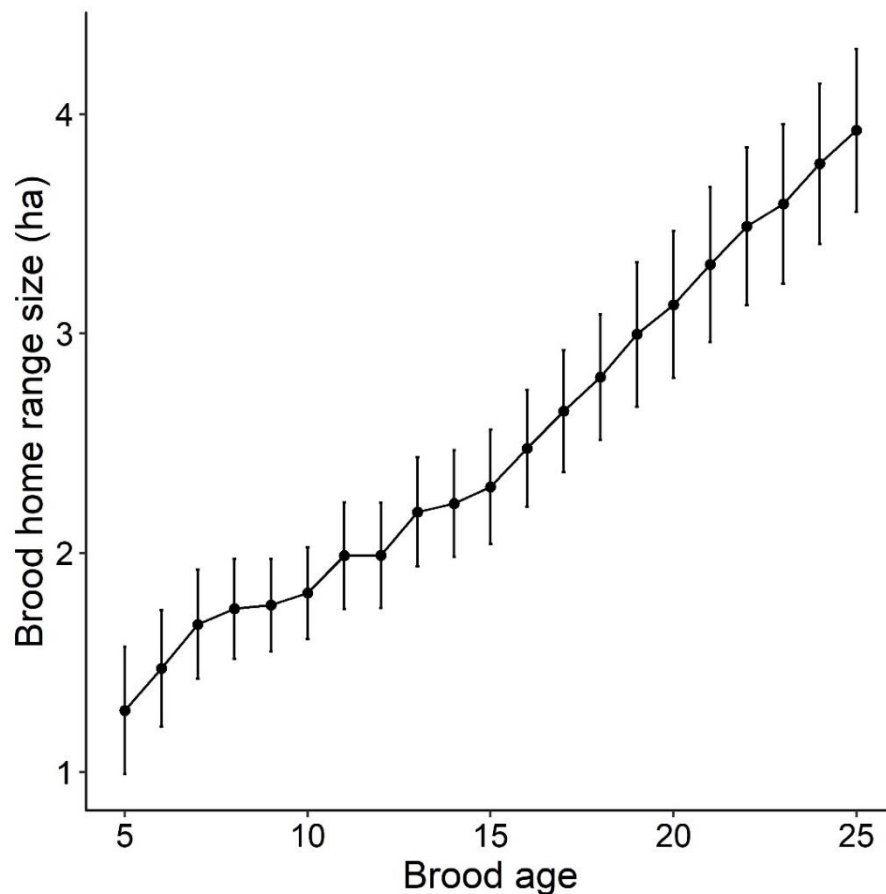


Figure 22. Cumulative home range size for piping plover broods as age increased, 2014–2019. Home ranges were only calculated for age classes where up to that point, the brood had at least five locations. Error bars represent standard error.

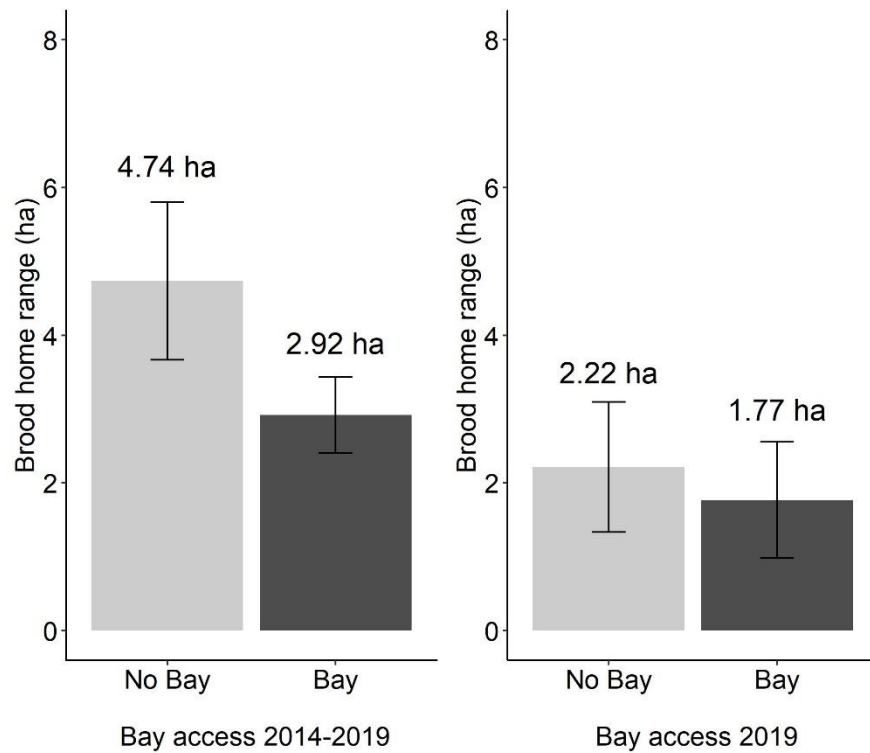


Figure 23. Average home range size among years (2014–2019) and in 2019, estimated using minimum convex polygons for broods that fledged at least one chick, of broods that did not have direct bayside access in the subsite of their nest (light gray) and the broods that did have direct bayside access in the subsite of their nests (dark gray). Error bars represent 95% confidence intervals.

Table 14. Brood home range size of broods that fledged at least one chick, by habitat type 2014–2019. Home ranges were created as minimum convex polygons for broods that had ≥ 5 locations.

Habitat Type	N	Mean home range area (ha)	SE	LCI	UCI
Breach fill	14	3.82	0.61	2.49	5.14
Manipulated overwash	28	3.42	0.84	1.70	5.15
Natural overwash	34	3.40	0.49	2.39	4.40
Restoration area	19	5.51	0.95	3.51	7.51
Other	73	4.22	0.65	2.92	5.53

Brood Movement

From 2014 to 2019, we recorded 1047 locations of broods on successive days. Average age of broods at observations was 10.9 days (SD = 7.79). Mean interval between observations was 1.72 days (SD = 1.43, median = 1.17). Mean daily movement was 131.68 m (SE = 4.83, median = 87.68). Movements between daily observations of broods were smaller, on average, for broods that had bay access ($\bar{x}$ = 105.16 m, SE = 5.47) than broods that did not across all years ($\bar{x}$ = 152.55 m, SE = 7.38; $W = 156970$, $P < 0.001$). Movement between daily observations was different among the five habitat groups (K-W $\chi^2 = 18.84$, $P < 0.001$). Broods in breach fills moved the least between daily observations and broods in natural overwashes moved the most between daily observations (Table 15).

Table 15. Average standardized distance (m/24 hr) moved by piping plover broods between successive daily observations, 2014–2019. Breach fills included portions of Narrow Bay West and Cupsogue West. Manipulated overwashes included portions of Narrow Bay West, Narrow Bay East, Pattersquash Overwash, and Cupsogue West. Natural overwashes included Old Inlet West, Old Inlet West Reference, Old Inlet East, and Bridge Overwash. Restoration areas included Great Gun and New Made.

Habitat	N	Distance (m/24hr)	SE	95% CI
Breach Fill	107	83.04	8.37	66.45–99.62
Manipulated Overwash	152	119.33	10.26	99.06–139.61
Natural Overwash	230	149.06	10.13	129.10–169.02
Other	482	141.04	8.32	124.68–157.40
Restoration Area	76	112.96	9.43	94.17–131.74

Discussion

Exclosures

Nest exclosures had the greatest effect on nest survival of the variables studied. During all years, exclosures were placed around nests during the laying period or after clutch completion. Typically, within the study area, exclosures were not installed around nests with fewer than four eggs to prevent nest abandonment. The placement of nesting exclosures is likely to reduce any detectable

effects of predators on daily nest survival unless a smart predator individual is able to reduce the effectiveness of the majority of exclosures. Predators have been known to cue in on exclosures (Murphy et al. 2003), and the managers of the plover breeding sites in the study area reacted to digging and entry into exclosures in varying manners. In 2015, Smith Point County Park had high fox density, and foxes, or potentially a single "smart fox," took some nests by climbing into the exclosures. Following these predation events, the exclosures were removed from all other nests at the county park. Once the exclosures were removed, the remaining nests, which were then unexclosed, were depredated. In 2018, a fox (which we believed to be the single fox in the area at this post-mange time) observed at Smith Point was digging at exclosures. After the digging incidents, exclosures were not placed on several nests throughout the eastern portion of Smith Point County Park in 2018 due to concern that exclosures would continue to attract predators and could lead to adult mortality. During this time, five unexclosed nests were depredated within Smith Point County Park. After these predation events, exclosures were installed around nests with at least three eggs to prevent future depredation, many of which hatched, although three were abandoned.

In one study examining plover nest exclosures, exclosing nests resulted in greater population growth rates than if nests were left unexclosed, although there is concern that nest exclosures may increase adult mortality (Cohen et al. 2016). A positive relationship between adult mortality and nest abandonment has been demonstrated (Neuman et al. 2004, Barber et al. 2010, Roche et al. 2010), and our resight rate of banded birds (55%) following nest abandonment from 2013–2019 is lower than the predicted annual survival rate of 0.69 ± 0.02 (see Part 2, Section 5). In their study of Great Lakes piping plovers, Roche et al. (2010) discovered that up to 70% of the nests monitored were abandoned due to the loss of at least one of the incubating adults. With a detection probability of 0.96 ± 0.02 (see Part 2, Section 5) for adults across all years of this study, it is likely that we would have seen banded adults following nest abandonment if they were still present in our study area. Therefore, adult mortality or emigration from the study area are the two most likely causes for the relatively low percentage of banded adults resighted after nest abandonment (Roche et al. 2010). Continuing to

exclosure Fire Island piping plover nests before they reach four eggs likely will reduce nest predation, improving overall productivity in the Fire Island piping plover population, but should be used with caution if nests are frequently being abandoned (Cohen et al. 2016).

Finally, we also found nest survival was negatively correlated with wind. Throughout the study, we noticed that storm events with high winds often were correlated with nest abandonment, with eggs being buried under sand and only the tops of eggs sticking out. However, because we rarely observed eggs actually blown out of nests, we suspect that the negative effect of wind on nest survival likely a result of wind improving our ability to detect that a nest had already been abandoned by covering the untended eggs with sand.

Predators

Nest survival during 2015–2018 was not related to red fox, raccoon or feral cat abundance. However, when considering all years of Fire Island data, nest survival was higher after the mange outbreak than it was before and during the outbreak, and in the models the effect size of the mange outbreak on nest survival was greater than the effect of nest exclosures. Lower chick survival was related to higher fox trap success and chick survival was higher in the post-mange years. Red foxes are well-known nest predators of plover nests (Patterson et al. 1991, Cohen et al. 2009, Doherty and Heath 2011), but chick mortality is challenging to document. Although we did not document foxes killing plover chicks, the relationship between red fox abundance and chick survival indicates that they may be responsible for some mortality.

Our results also suggested that the red fox population crash due to mange resulted in higher chick survival and higher reproductive output in post-mange years compared to pre-mange years despite the presence of other avian and mammalian predators in the study area (see Part 2, Section 7 for information on other predators). However, the decline in the red fox population did not explain all variation in reproductive output, as plover nesting density, temperature and habitat were also influential to chick and nest survival. The change in the effect of nesting density on both chick and

nest survival once the mange variables were added in the models, suggests that there may be some interaction occurring between predation by foxes and nesting density as would be expected predation was density dependent. The effect of predator removal and exclusion has been documented in plovers and other similar taxa. For example, on the Missouri River, owl trapping was followed by increased chick survival and the data suggested predation on chicks was density dependent (Catlin et al. 2011a). 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. Future monitoring of plovers on Fire Island may benefit from aerial predator monitoring in addition to continued terrestrial predator monitoring to be able to link reproductive output to other predator taxa. These results illustrate the importance of a long-term data set to understand temporal trends in vital rates, and the importance of comparing several potential drivers of vital rates into population models.

Density

Nest survival was positively correlated with nesting plover density, and this is likely because we had a positive trend in nest survival following Hurricane Sandy, and density increased in nearly all management areas over the same period until 2019. Chick survival, however, was negatively correlated with plover-nesting density. Plovers are territorial and compete for space during both the nesting and the brooding period (Elliott-Smith and Haig 2004). Higher plover nesting density can lead to intra-specific aggression, but can also aid in the ability of predators to develop a search image for abundant prey (Whitfield 2003, Hunt et al. 2019a). Although the decline in red foxes did not seem to increase depredation of nests and chicks by raccoons or feral cats, there are other possible predators on the island that may have developed a search image for shorebirds as population density increased. Moreover, an increase in density likely leads to an increase in plover interspecific strife which is obvious to human observers and may lead to increase in detection probabilities by predators and reduced anti-predator vigilance by plovers. We observed an increase adult mortality by aerial

predators and this may have extended to chicks. However, chicks are smaller than adults making their carcasses difficult to detect and easier to swallow whole.

Habitat

Although restoration areas had lower nest survival than other areas, when all other variables were considered, being in a restoration area did not influence chick survival. In contrast, manipulated and natural overwashes had no relationship to nest survival, but chicks within manipulated and natural overwashes had higher survival. The differences observed between habitat types were likely influenced by local density, vegetation characteristics, and access to quality foraging habitat. Lower nest survival in the restoration areas may be due to specific management decisions regarding exclosure use. Specifically, the decisions to remove exclosures in 2015 when an individual fox was entering exclosures, and to not exclose nests in 2018 following observed canine digging around exclosures. Both instances led to high predation rates of Smith Point nests, which included the restoration areas. Overwashes had greater invertebrate abundance than breach fills and restoration areas, which could have promoted higher chick survival. Further, manipulated overwashes in particular had lower nesting densities than breach fills and natural overwash, although they were higher than restoration areas (Bellman 2018).

Bay access for chicks seemed to decrease the home range size of broods, particularly in early years of the study. There could be several explanations for this finding as the distance to bay was not related to chick home range size. Broods may not need to move as much to access adequate forage on the bayside, because the invertebrate abundance is richer (Part 2, Section 6). Nesting density may also be greater in bayside areas, constraining the available space for broods to access (see Part 2, Section 3). That the difference in home range size between the habitat types was smallest in 2019 when density was greatest suggests that local density may be playing a role in such habitat effects. However, there was little difference in home range size by categorical habitat type. Chicks in restoration areas had larger home ranges and broods moved less in breach fills and more in natural

overwashes. Assessing both descriptors (movement and home range size) of space use is thus important to understanding how plover broods use the landscape.

Cupsogue

The Cupsogue study area had to be removed from models in order to explicitly compare chick and nest survival between pre- and during the mange outbreak to after the mange outbreak, because we did not have information about mange in Cupsogue. Reproductive output was consistently lower at Cupsogue relative to the rest of the study area. Although we do not understand the predator community at Cupsogue, we have found that human disturbance is influential to chick survival in this system (DeRose-Wilson et al. 2018). Cupsogue broods are likely contributing to lower chick survival in the breach fills as Cupsogue chicks make up about half of the breach-fill brood sample size. We would expect that the access to bayside foraging habitat at both breach fill sites would improve chick survival (Patterson et al. 1991, Elias et al. 2000, Cohen et al. 2009). However, in Cupsogue, high human use of the bayside in some years prevented chick from foraging in the preferred habitat. Moreover, higher plover nesting density in the breach fills may also contribute to lower reproductive output. Two-sided habitats (where dry sand spans from the ocean- to bay-side of an island), like the breach fills in this study, have been shown to have higher nesting plover density (Cohen et al. 2009), and the breach fills had some of the highest densities in our study area, particularly the Narrow Bay Breach Fill (Bellman 2018). In addition, least cost distance to ocean and bay both related positively to chick survival when all of the data were included, however removing Cupsogue dampened this effect. This suggests that at least part of the trend of higher survival farther from foraging habitat is driven by Cupsogue, where birds may survive better when they are in the symbolic fencing and away from beachgoers.

Overall, of the variables we looked at, the primary drivers of reproductive output seem to be nesting plover density and predators, specifically red foxes. However, human disturbance, which we did not include in our models, also has an effect on reproductive output (DeRose-Wilson et al. 2018).

The direct estimation of population parameters, such as reproductive output and its constituent elements, nest and chick survival, are essential to understanding change in breeding populations of threatened species (Purvis et al. 2000). Reproductive output in our population contributes to population growth (Robinson et al. 2020*b*), therefore it is essential that we try to maximize the reproductive output on Fire and Westhampton Islands to maximize the rate at which the population grows toward the carrying capacity of the study area. 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 (Lengyel 2006, Nichols and Kaiser 1999). In future analyses, we hope to assess chick habitat selection and behavior to obtain a more complete picture of the mechanistic drivers of reproductive output on Fire Island.

Section 5: Compare the relative contribution of local growth (natal recruitment) vs immigration in population growth associated with new habitats

Introduction

Changes in population vital rates as a function of population density (density-dependence), are required for population regulation (Royama 1977, Turchin 1990, Newton 1998, Coulson et al. 2008). In such regulation, some or all vital rates (reproductive output, survival, immigration, emigration; Coulson et al. 2008, Gamelon et al. 2016, Andersen et al. 2017) decline at higher population densities and increase at lower densities, leading the population back to a maximum sustainable level, or carrying capacity. Density dependent responses can occur due to site-dependence, interference, crowding, and predation, and are particularly notable in territorial species (Rodenhouse et al. 1997, Nevoux et al. 2011). An increase in habitat following a disturbance event is likely to release a population from existing negative density-dependent processes by decreasing population density.

When habitats change following disturbance events, increasing the quantity and/or quality of that habitat and lessening density-dependent constraints, the composition of the breeding cohort may change, altering immigration and local recruitment rates. Broadly, a nesting population can be composed of 1) birds that returned to the area in which they previously nested (adult returners), 2) birds that immigrated from other areas (immigrants), and 3), yearlings that hatched in the population and returned to breed (natal recruits; Lampila et al. 2006, Million et al. 2019). Newly created habitat may change the contribution from each cohort, such as by an increase in immigrants or natal recruits, which can settle due to newly opened territories.

For piping plovers, population changes often follow habitat-creating events, such as major floods or hurricanes (Cohen et al. 2009, Hunt et al. 2018*a*, Catlin et al. 2019*b*, Robinson et al. 2019). However, the demographic drivers of these changes may vary. Potential density-dependent reasons for these changes could be increased immigration into the newly available habitat, increased reproductive output leading to more natal recruits, or increased adult and post-fledgling survival

(Cohen et al. 2009, Catlin et al. 2015, Hunt et al. 2018a). Immigration rates often are unknown as they are difficult to measure. Even though immigration is more often studied in birds relative to mammals (Million et al. 2019), we still lack detailed studies on the role of immigration in the population dynamics of many birds, including the piping plover. Studies on the Atlantic Coast population have indicated that immigration is influential in changing a local piping plover population, but it has yet to be quantified (Cohen et al. 2009, Weithman et al. 2019). If immigration is a primary driver of population growth, it is important to understand how to focus management to maximize this process. To understand the relative contributions of local recruitment and immigration to population change on Fire and Westhampton islands, we 1) determined the composition of the nesting adult cohort following Hurricane Sandy, 2) compared use by each nesting class to available habitat to determine if any particular habitat could be driving population change, and 3) assessed adult and hatch-year survival to determine if increased survival could be leading to observed population change.

Methods

Immigration and recruitment

In our study population, we were able to band most chicks and adults in each year from 2013–2019; therefore, we estimated immigrants using the number of newly banded adults in a year. In 2020, no banding occurred, therefore we considered the number of unbanded birds to be the number of immigrants. While great effort is exercised to confirm individual birds to nests each year, we were not able to confirm each bird as a nester in each year due to trap aversion or nests in denser vegetation particularly in 2019 and limitations of site accessibility and visitation frequency in 2020. Here, we assume that our detection was not biased towards any specific nesting class. If individuals that hatched in the study population returned to breed 2+ years after hatching, we counted them as natal recruits in the year of first breeding. Although a population is likely to have floater adults that could not obtain either a mate or a breeding territory, they do not contribute to the reproductive output in a population and were not included in annual pair counts, and thus they were not included here.

Using banded and known-age birds, we estimated immigration and natal recruitment for 2014–2019. We estimated immigration rate using a Pradel (1996) model in Program Mark (White and Burnham 1999). The parameters estimated from the Pradel model are apparent survival, resight rate, and fecundity rate. We interpreted fecundity as an estimate of immigration rate (# immigrants in $t+1$ per individual in year t), which included natal recruits and immigrants. To estimate annual immigration rates, we fit a single model holding apparent survival and resight rate constant, as prior studies indicated that adult survival and detection probability were relatively constant, (Catlin et al. 2015, Weithman et al. 2019). For immigration rate in 2014 and 2015, the estimate included only the eastern portion of the study area (Old Inlet West to Cupsogue). Starting in 2016, estimates of immigration rate also included the Democrat Point site, as birds were first banded there in 2015 and thus we could first estimate the breeding cohort composition in 2016. We estimated annual local recruitment as the number of individuals banded as chicks in years prior that returned to breed for the first time in the population in a given year. In addition to immigration rates, we assessed how many of the newly banded individuals (2014–2019) or unbanded individuals (2020; immigrants), local recruits, and returning nesters settled into new habitats (breach fill, manipulated overwash, natural overwash, restoration area, and other, see Part 1, Table 1 for details on habitat definitions) created following Hurricane Sandy from 2014–2020.

To determine if immigrants, natal recruits, and returning nesters selected for or against the habitat types, we compared percent area of each habitat type available and the percent each habitat type used by the classes of nesting plovers. To estimate amount of available habitat, we included patches of dry sand in the eastern study area in 2014–2019 (Old Inlet West to Cupsogue) and 2020 (Old Inlet West to Great Gun Restoration Area) of at least 1m² following the same methods in Part 2, Section 3. We only conducted this analysis for the eastern study area because we had data for each year of the study, and habitat types were only located in this part of the site. We then determined the amount of dry sand used within each of the habitat areas, as defined by delineated ocean-to-bay overwash and USACE-provided shapefiles. We calculated the proportion of habitat use as the

proportion of returning adult nesters, natal recruits, or immigrants in each habitat type. We conducted a chi-squared test to determine if there was overall selection occurring within nesting classes and compared 95% confidence intervals on proportion of use to availability to determine selection for or against particular habitat types (Byers et al. 1984, Catlin et al. 2011 *b*). If a breeding class did not nest in a habitat type within a year, we interpreted it as avoidance. We completed this analysis for each year, 2014–2020, to evaluate if selection changed as plover dynamics and island characteristics changed.

Survival and site fidelity

To estimate true survival of piping plovers in the Fire Island study area, we used the Barker live-dead encounter model (Barker 1997). The Barker model uses supplemental (off-site) resightings to distinguish permanent emigration from mortality for a more accurate estimate of survival than is available when just considering return rate. Our primary interest for this report was in true survival (S) of first year (hatch to first year b) and adult (after first breeding season) piping plovers. Other parameters that we estimated using this model were detection probability (p), probability of being reported dead during the supplemental period (r), the probability of being resighted during and surviving the supplemental period (R), the probability of being resighted during the supplemental period and dying (R'), site fidelity (F), and the probability of returning to the study area after emigration (F'). We fixed r to 0, as we did not have any reports of dead individuals during the supplemental period. We modeled variation in all of the parameters, other than r , with year and age. We tested for overdispersion ($\hat{c}$) using a model with age and year variation in all models and corrected for overdispersion if confidence intervals $\hat{c}$ did not overlap 1. We used annual pre-fledge chick survival estimates from Part 2, Section 4 and our annual estimates of first-year survival from the Barker model to derive post-fledging survival, survival from fledging until the following year. Post-fledge survival is first-year survival divided by pre-fledge survival (Catlin et al. 2015, Weithman et al. 2019).

Results

Immigration and recruitment

In 2020, 22 of 142 (15%) nesting adults were not confirmed to be returners, recruits, or immigrants due to limitations with site accessibility and frequency of visitation. Of unknown breeding birds, 10 nested within the western study area (Democrat Point to Lighthouse Tract), and 12 in the eastern study area (11 in the Western Wilderness Area and one at Narrow Bay East). Therefore, 120 breeding individuals in 2020 were used in this analysis.

From 2014 to 2020, the breeding population included 31–54% returning nesters annually (Table 16). The remainder of the birds that nested in the study area were unbanded birds that were captured during the year (2014–2019) or remained unbanded (2020; immigrants; 34–63%) or that hatched in the study area the year before (natal recruits; 6–25%). The Pradel model resulted in estimates of combined natal recruitment and immigration between 0.53 and 0.87 immigrants in year $t+1$, per individual in year t from 2014–2019.

Table 16. Breeding adult piping plovers divided into the categories of returning nesters, local recruits, and immigrants. Numbers for 2014 and 2015 only include the eastern study area (Fire Island National Seashore Wilderness Area to Cupsogue Beach County Park). Numbers for 2016–2019 include the entire study area (Robert Moses State Park to Cupsogue Beach County Park). 2020 numbers include Robert Moses State Park, Fire Island National Seashore, and Smith Point County Park. Immigration rate was not calculated in 2020 due to lack of regular adult surveys.

Year	Returning Nesters	Natal Recruits ^a	Immigrants ^b	Immigration Rate ($\pm$ SE ^c)
2014	17 (47%)	2 (6%)	17 (47%)	0.62 (0.20)
2015	20 (53%)	5 (13%)	13 (34%)	0.52 (0.16)
2016	21 (31%)	4 (6%)	42 (63%)	0.87 (0.18)
2017	32 (38%)	16 (19%)	36 (43%)	0.67 (0.12)
2018	46 (43%)	17 (16%)	44 (41%)	0.65 (0.11)
2019	60 (41%)	36 (25%)	50 (34%)	0.75 (0.11)
2020 ^d	65 (54%)	21 (18%)	34 (28%)	-

^a Natal recruits refers to individuals that were hatched as chicks in the study area and returned in a following year to nest.

^b Immigrants refers to the individuals that were newly banded and any birds that were known to have hatched outside of the study area that then nested within our study area.

^c Immigration rate estimated using a Pradel (1996) model in Program MARK. Immigration rate represents the # of immigrants in year $t+1$, per individual in year t .

^d 2020 numbers only include 85% of breeding adults. The other 15% were not resighted for bands, therefore, could not be identified as returning nesters, natal recruits, or immigrants.

Breach fills made up the smallest proportion of the eastern study area, ranging from 2.6% to 3.2% during 2014–2019 (including Cupsogue Breach) and 1% in 2020 (excluding Cupsogue Breach). Restoration areas made up 10.3% to 25.0% of the dry sand in the eastern study area, natural overwashes made up 10.3% to 15.7% of the dry sand, and manipulated overwashes made up 15.1 to 21.4% of the available dry sand. Other habitats made up the greatest proportion of the available dry sand in the eastern study area, ranging from 42.3% to 61%.

In all years combined, 68% of returners nested in newly created habitats (Table 17). They nested in manipulated overwashes (24%) and natural overwashes (23%) the most, followed by restoration areas (11%) and breach fills (10%). The remaining 32% of returners nested in “other” habitat (Table 17). Returners exhibited selection for or against specific habitat types most frequently out of the three nesting classes (Figure 24). Returners selected breach fills in 2015 and 2017, manipulated overwashes in 2016 and 2018, and natural overwashes from 2017–2019. Returners selected all new habitats in proportion to their availability in 2020 and avoided “other” habitat in all years (Figure 24).

Table 17. The number of returners that nested in new habitats on Fire Island and at Cupsogue Beach County Park following Hurricane Sandy and subsequent habitat alteration.

Year	Total # Returners	Natural Overwash	Manipulated Overwash	Breach Fill	Restoration Area	% Returners in other, pre- Sandy Habitats	% Returners in New Habitats
2014	17	4 (24%)	7 (41%)	0	NA	6 (35%)	65%
2015	20	3 (15%)	7 (35%)	5 (25%)	1 (5%)	4 (20%)	80%
2016	21	6 (29%)	8 (38%)	4 (19%)	0	3 (14%)	86%
2017	32	8 (25%)	7 (22%)	7 (22%)	2 (6%)	8 (25%)	75%
2018	46	15 (33%)	12 (26%)	3 (7%)	3 (7%)	13 (28%)	72%
2019	60	13 (22%)	12 (20%)	4 (7%)	11 (18%)	20 (33%)	67%
2020 ^{ab}	65	12 (18%)	9 (14%)	2 (3%)	11 (17%)	31 (48%)	52%
Total	261	61 (23%)	62 (24%)	25 (10%)	28 (11%)	85 (32%)	68%

^a Numbers in 2020 only consisted only of the Fire Island study area and did not include Cupsogue Beach County Park.

^b 2020 numbers only include 85% of breeding adults. The other 15% were not resighted for bands, therefore, could not be identified as returning nesters, natal recruits, or immigrants.

Natal recruits made up the smallest of these three cohorts (6-25% over the years, Table 18). In all years combined, 59% of recruits nested in newly-created habitats (Table 18). They nested in restoration areas (28%) and natural overwashes (13%) the most, followed by manipulated overwashes (10%) and breach fills (9%). The remaining 41% of recruits nested in "other" habitat (Table 18). Overall, recruits nested in restoration areas in every year they were available and more than expected based on availability in 2015, 2018, and 2019. Recruits avoided nesting in breach fills in 2017 and 2018 but selected for them in 2020. No natal recruits nested in breach fills in 2014, 2015, and 2018, manipulated overwashes in 2016 and 2020, natural overwashes in 2014, 2015, and 2019, and "other" habitat in 2015 and 2020. During 2014–2018, natal recruits selected for natural overwashes in proportion to their availability, selected against them in 2019, yet selected for them in 2020 (Figure 24).

Table 18. The number of natal recruits in the population that nested in new habitats on Fire Island and at Cupsogue Beach County Park following Hurricane Sandy and subsequent habitat alteration. Recruits were banded as chicks in the year prior and returned to breed in the study area.

Year	Total # Returners	Natural Overwash	Manipulated Overwash	Breach Fill	Restoration Area	% Returners in other, pre-Sandy Habitats	% Returners in New Habitats
2014	2	0	1 (50%)	0	NA	1 (50%)	50%
2015	5	0	2 (40%)	0	3 (60%)	0	100%
2016	4	1 (25%)	0	1 (25%)	1 (25%)	1 (25%)	75%
2017	16	3 (19%)	3 (19%)	3 (19%)	3 (19%)	4 (25%)	75%
2018	17	1 (6%)	2 (12%)	0	7 (41%)	7 (41%)	59%
2019	36	1 (3%)	2 (6%)	3 (8%)	9 (25%)	21 (58%)	42%
2020 ^{ab}	21	7 (33%)	0	2 (10%)	5 (24%)	7 (33%)	67%
Total	101	13 (13%)	10 (10%)	9 (9%)	28 (28%)	41 (41%)	59%

^a Numbers in 2020 only consisted only of the Fire Island study area and did not include Cupsogue Beach County Park.

^b 2020 numbers only include 85% of breeding adults. The other 15% were not resighted for bands, therefore, could not be identified as returning nesters, natal recruits, or immigrants.

In all years combined, 45% of immigrants nested in newly created habitats (Table 19).

Immigrants nested in manipulated overwashes (15%) and restoration areas (14%) the most, followed by natural overwashes (12%) and breach fills (4%). The remaining 55% of immigrants nested in "other" habitat (Table 19). Based on availability, we would have expected more immigrants to nest in "other" habitat every year except 2019 and 2020. In 2019 and 2020, immigrants nested in "other" habitat proportional to its availability. Except for "other" habitat, which was avoided, immigrants nested with a frequency we would expect based on availability in every habitat type across all years until 2019.

Immigrants avoided breach fills in 2019 and 2020 and manipulated overwashes in 2020 (Figure 24).

2020 was the only year in which immigrants selected for a habitat, as they nested in restoration areas

more than would be expected based on the amount of dry sand nesting habitat available (Figure 24).

See Appendix A (figures A-1–A-7) for year-specific selection plots and statistical tests.

Table 19. The number of individuals that immigrated into the population and nested in new habitats on Fire Island and at Cupsogue Beach County Park following Hurricane Sandy and subsequent habitat alteration.

Year	Total # Immigrants	Natural Overwash	Manipulated Overwash	Breach Fill	Restoration Area	% Immigrants in other, pre-Sandy Habitats	% Immigrants in New Habitats
				2		6 (35%)	
2014	17	3 (18%)	6 (35%)	(12%)	NA		65%
2015	13	1 (8%)	5 (38%)	1 (8%)	3 (23%)	3 (23%)	77%
2016	42	5 (12%)	7 (17%)	1 (2%)	4 (10%)	25 (60%)	40%
2017	36	8 (22%)	6 (17%)	3 (8%)	7 (19%)	12 (33%)	67%
2018	44	2 (5%)	7 (16%)	3 (7%)	6 (14%)	26 (59%)	41%
2019	50	7 (14%)	5 (10%)	0	2 (4%)	36 (72%)	28%
2020 ^{ab}	34	3 (8%)	0	0	10 (29%)	21 (63%)	38%
Total	236	29 (12%)	36 (15%)	10 (4%)	32 (14%)	129 (55%)	45%

^a Numbers in 2020 only consisted only of the Fire Island study area and did not include Cupsogue Beach County Park.

^b 2020 numbers only include 85% of breeding adults. The other 15% were not resighted for bands, therefore, could not be identified as returning nesters, natal recruits, or immigrants.

	Returners						
	2014	2015	2016	2017	2018	2019	2020
Breach Fill	0	+	=	+	=	=	=
Manipulated	=	=	+	=	+	=	=
Overwash	=	=	=	+	+	+	=
Natural Overwash	=	=	=	+	+	+	=
Restoration Area	NA	=	0	=	=	+	=
Other	-	-	0	0	-	-	-

	Natal Recruits						
	2014	2015	2016	2017	2018	2019	2020
Breach Fill	0	0	=	=	0	=	+
Manipulated	=	=	0	=	=	=	0
Overwash	=	=	=	=	=	=	=
Natural Overwash	0	0	=	=	=	-	+
Restoration Area	NA	+	=	=	+	+	=
Other	=	0	=	-	-	=	0

	Immigrants						
	2014	2015	2016	2017	2018	2019	2020
Breach Fill	=	=	=	=	=	0	0
Manipulated	=	=	=	=	=	=	0
Overwash	=	=	=	=	=	=	=
Natural Overwash	=	=	=	=	=	=	=
Restoration Area	NA	=	=	=	=	=	+
Other	-	-	-	-	-	=	=

Figure 24. Selection by returners, natal recruits, and immigrants in each habitat type. Plus signs represent more nesters than expected in a habitat based on availability. Minus signs represent fewer nesters than expected in a habitat based on availability. If a habitat had no nesters in it that year, they were given zeroes. Restoration areas were not created until 2015, so were denoted NA in 2014. Blue indicates avoidance, with the lightest blue indicating no use whereas slightly darker blue indicates statistical avoidance, yellow indicates selection for a habitat type, and grey indicates use in proportion to what is available.

Survival and site fidelity

The top model from the survival and fidelity analysis indicated temporal variation in survival for first-year birds, a constant adult survival rate for all years, and an age effect on site fidelity (F) (Table A-1). Point estimates of first-year survival varied each year of the study, with high years of first-year

survival relating to years of high chick survival (Figure 25). Adult survival ($S = 0.69 \pm 0.02$) was within the range of past studies of adult piping plover survival and is within the confidence intervals of our estimate from 2013–2018 (Hermanns et al. 2018). Site fidelity for adult birds ($F = 0.92 \pm 0.02$) was higher than for first-year birds ($F = 0.76 \pm 0.04$), and first-year site fidelity increased with the addition of the 2019 data. Detection probability was constant over both ages and across all years ($p = 0.96 \pm 0.02$). Post-fledgling survival (hatch to fledging), survival from fledging to returning the following year, varied among years (Figure 26). We observed the highest rate of post-fledgling survival in 2013 fledglings.

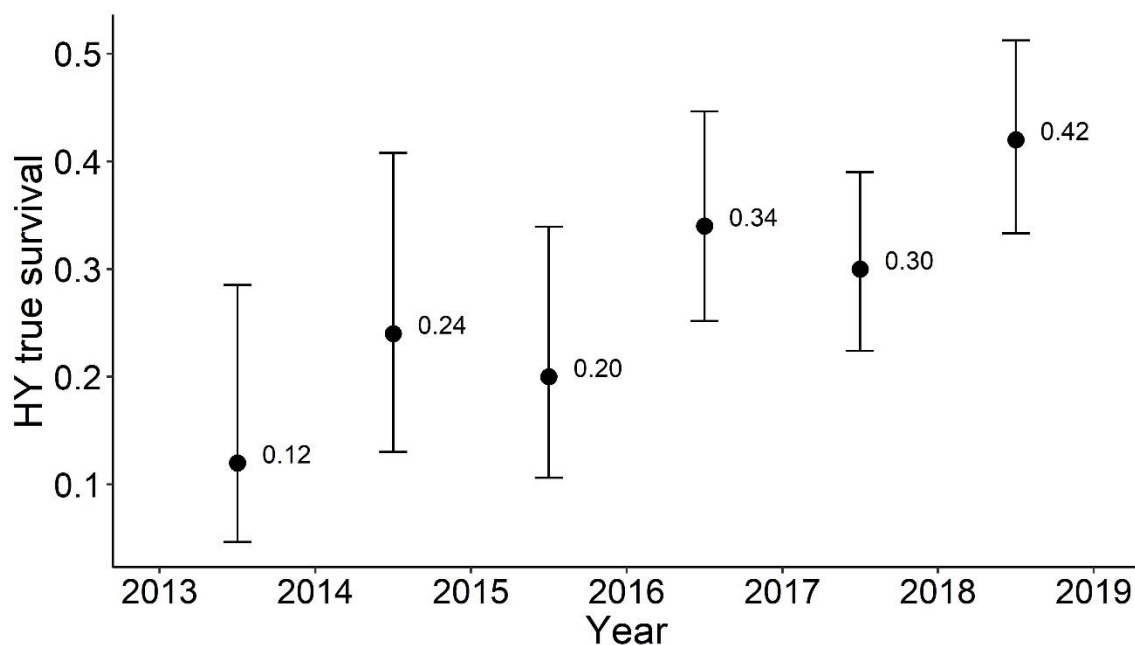


Figure 25. True survival (S) of first year (from hatch to year 1) piping plovers on Fire Island from 2013 to 2019. Estimates are from the top model with an additive effect of year and age. Error bars represent 95% confidence intervals.

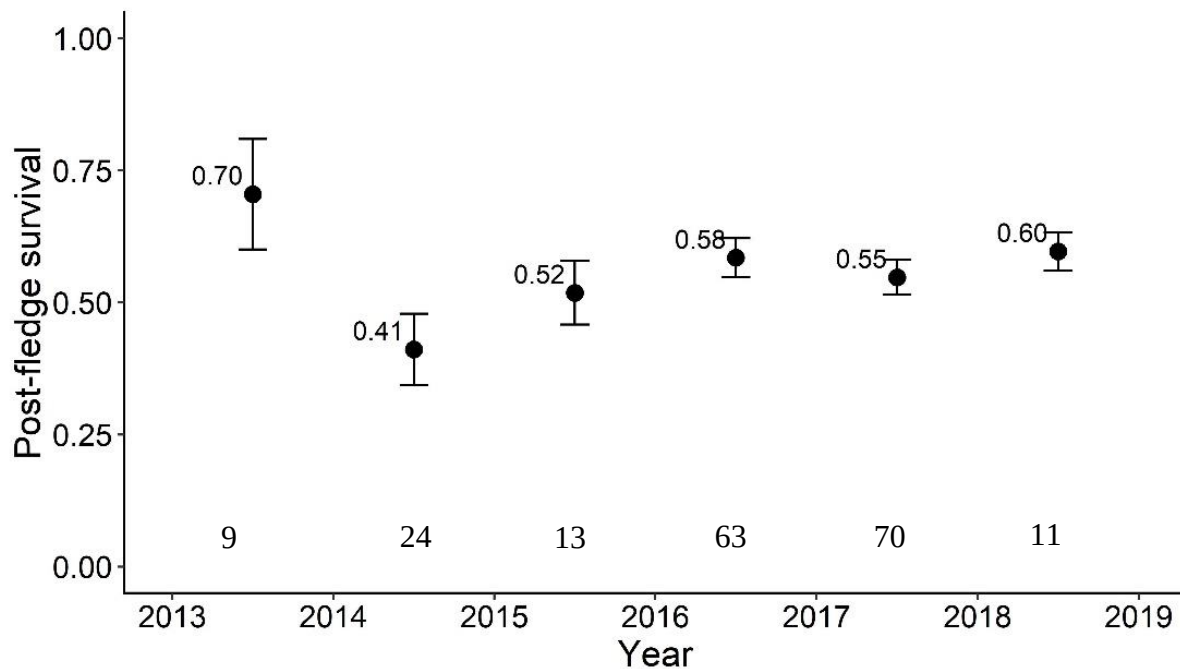


Figure 26. Post-fledge survival of piping plovers on Fire Island, New York from 2013 to 2019. Post-fledge survival is the survival from fledgling to returning the following year, and is calculated by dividing first year survival by pre-fledge chick survival. Error bars represent 95% confidence intervals. Numbers above x-axis represent number of fledglings.

In 2018, six banded adult mortalities were confirmed either by discovering carcasses of adults or by procuring bands or flags from a predator scat sample collected during field surveys. All mortalities were identified as predation. At least one mortality was caused by a peregrine falcon (*Falco peregrinus*) and one mortality was later confirmed to be caused by a cat (*Felis catus*) via mitochondrial DNA sequencing of the scat sample we collected (Part 3, Section 4). In 2019, we confirmed two adult mortalities in our study area. The flag leg of one adult was found outside of an exclosure and was likely depredated by a peregrine falcon based on field sign. We discovered evidence that at least one peregrine falcon was frequenting the area and using exclosures as perches, as several exclosures had bones, feathers, and entrails in the vicinity. The carcass of another banded adult was found in vehicle tire tracks on the driving portion of open beach in NBW. The cause of mortality was not determined, but following its discovery, a nest within 250m was abandoned. Unfortunately, the adult was not confirmed to the nest so we cannot be certain that the two incidents are related.

Discussion

Here, we detected patterns in plover nest locations that illustrated selection and avoidance of certain habitat types by comparing the choices that adult plovers made when nesting in the study area compared to the amount of each habitat that was available on the landscape. Habitats such as backshore and barrier interior that were classified as “other” for these analyses, and were present before Hurricane Sandy, made up the greatest proportion of available plover nesting habitat based on our dry sand classification. However, during this study, birds nested in pre-Hurricane Sandy areas at lower proportions when compared to the newly created habitat in each year. When combined, natal recruits, immigrants, and returners nested in habitats created since Hurricane Sandy 57% of the time and only nested in “other” habitat 43% of the time despite the fact that “other” comprised 42–61% of the available nesting habitat depending on the year, suggesting that overall, plovers preferred newly-created habitats.

All three classes of nesting piping plovers avoided “other” habitats or selected for the habitats created following Hurricane Sandy, relative to what was available. Many of these areas were overwashed, or were created to appear like overwash and, thus, had greater backshore widths and wider, open sand nesting habitat. Open sandy habitat, like that created by Hurricane Sandy, can assist nesting plovers in detecting predators and can play a role in the camouflage of their eggs and chicks (Fraser and Catlin 2019). Alternatively, habitat fragmentation and being closer to dense vegetation may make the pre-Sandy habitats less attractive to all classes of nesting birds. These pre-Sandy areas also have less distance between the high tide line and the toe of the dune, which makes nests more susceptible to flooding compared to all of the post-Hurricane Sandy habitats. Although for this analysis, we considered every patch of dry sand greater than 1-m² available, some of this habitat may be unsuitable to nesting birds, however much of the unsuitable habitat is likely to be the pre-Hurricane Sandy “other” habitat (Walker et al. 2019).

In 2016, we observed the highest immigration rate of all the three years examined, although the count of immigrants may be a slight over-estimate due to a small number of birds that did not

get banded in the year prior due to early nest failure or trap aversion, although overall there were few to no unbanded adults in each year. This relatively high immigration rate may have been due to low nest and chick survival in 2015, causing adults to not return to nest on Fire Island and opening up habitat for new nesting birds, especially as 2016 had the lowest proportion of returning nesters and natal recruits in the population. However, the proportion of the population that was composed of immigrants, and the proportion of immigrants in new habitats has declined in recent years. This may suggest that the Fire and Westhampton islands piping plover population is nearing the carrying capacity of its habitat, resulting in less available space for new birds. The new habitats may also be reaching their carrying capacity.

Overall, immigration greatly contributed to the 186% population increase that occurred on Fire Island and Westhampton Island between Hurricane Sandy and 2019. While the population decreased in 2020, immigrants still made up at least 28% of the nesting population. Through 2020, immigrants generally selected storm-created and human-created habitats in proportion to their availability and generally avoided "other" habitats (largely ocean backshore) until 2019 and 2020 when they selected "other" habitats in proportion to their availability. Increasing nesting density likely decreases the habitat available to immigrants, and therefore it is possible that breach fills have become too dense for new birds to obtain territories while returning adults were remaining faithful to their nest sites, which could be why we did not observe any immigrants nesting in the breach fills in 2019 and 2020. Immigrants only exhibited selection for a specific habitat in 2020, in which they selected for restoration areas. The only restoration area used by plovers in 2020 was Great Gun restoration area, which had undergone vegetative removal prior to the 2020 breeding season. Mechanical removal of vegetation likely minimized dry sand fragmentation within the restoration area, which could serve beneficial to nesting plovers in avoiding predators, especially as habitat fragmentation and revegetation continued to increase elsewhere in the study area. In all years prior to 2020, immigrants used habitat in proportion to what was available, therefore a good way to increase and maintain immigration into the population is to maintain open, wide, sparsely vegetated sand. However,

selection patterns of immigrants in future years will be paramount in considering how immigrants select for habitats in a stabilizing population with locally high nesting densities.

Similarly, on the Missouri River, immigration declined as nesting density increased (Catlin et al. 2015). On the Outer Banks of North Carolina, the small population in the southern extent of the Atlantic Coast range, population size is likely sustained by immigration (Weithman et al. 2019). In the Great Lakes plover population, immigration is correlated with population growth, although less so than survival and fecundity (Saunders et al. 2018). This difference is likely due to the spatial scale differences between the Great Lakes population, which is an entire sub-population, as opposed to Fire Island and Westhampton Island, which is only a small portion of the Atlantic Coast population.

Natal recruits, or birds that hatched in our study area that returned the following year, nested in each habitat, every year, almost as much as we would expect based on area of habitat. However, in 2020, natal recruits selected for breach fills and natural overwashes more often than expected based on availability. Given that natal recruits either selected these habitats proportional to availability or selected against them in years prior, this was a notable result. One pair of second-year birds nested in Narrow Bay West, and seven nested at Old Inlet East, a surprising finding given that in 2019, natal recruits selected against natural overwashes. Natal recruitment tended to be variable and higher following years of higher chick survival. Fledglings prospect for potential nesting sites prior to departing for the wintering grounds (Davis et al. 2017), thus natal recruits habitat selection could have been driven by observations of high reproductive success and conspecific adults selecting for post-Hurricane Sandy habitats during their hatch year. Similar to what we have seen on Fire Island, across avian taxa, the contribution of immigration to population growth generally is higher than the contribution of natal recruitment (Million et al. 2019).

That we found adult survival to be constant among years is generally consistent with many avian populations (Saether et al. 2002, Lampila et al. 2006). Sufficient adult survival, which is usually found to have high sensitivity relative to population change (Calvert et al. 2006), is unlikely to be allowing the near doubling of the population in the Fire and Westhampton islands study area. Hatch-

year survival generally tracks the trends for pre-fledging chick survival (Part 2, Section 4), suggesting that pre-fledging chick survival is primarily driving the annual variation in this parameter. For this report, we have used both a different model and a differing model structure to estimate chick survival, and thus derived estimates of post-fledgling survival vary from previous reports, in particular the 2013 estimate. Years with low sample size, such as 2013, are vulnerable to being altered by the overall trend in the data, which is overall higher chick survival. We also changed this model such that we use a 5-day encounter window, and use the number of eggs that hatched rather than the number of chicks ever observed as the first encounter. Only using the chicks observed certainly biased chick survival high in the past.

A population that experienced exponential growth, such as Fire Island from 2013–2019, is likely to have very different dynamics than a stationary population (Schaub et al. 2013, Million et al. 2019). Following Hurricane Sandy, immigration was the primary correlate with population growth, although reproductive output is positively associated with population change (Robinson et al. 2020*b*). While demographic estimates were not possible given the constraints of our study in 2020, future monitoring of this population is needed to understand the variation in the contribution to population change of each demographic parameter as vegetation increases, suitable habitat declines, and the population stabilizes.

Section 6: Compare prey densities at several habitat types

Introduction

It is important to understand the effect of hurricanes and other environmental perturbations on threatened and endangered species. Disturbance on the landscape can manifest in changes to both the biotic and abiotic environment and can occur at fine and broad scales. Barrier islands, as narrow, dry sand islands that lay parallel and close to the mainland are particularly susceptible to environmental changes. Following an environmental event to a barrier island, such as a hurricane, modifications such as dune building often are conducted to protect the mainland from flooding in future events or to improve the beach for recreational purposes after hurricane-related changes. These natural and engineered changes can affect wildlife that are native to these ecosystems in both direct (e.g., loss or creation of nesting habitat space) and indirect (e.g., changes in food availability and distribution) ways.

Breaches and overwashes, such as those resulting from Hurricane Sandy, can create intertidal flats that serve as foraging habitat for shorebirds (Cohen et al. 2009). Breaches and overwashes can alter the invertebrate prey base that was present in an area or open up new areas for colonization by invertebrates. However, piping plovers' invertebrate prey base also can be altered when sand is placed in areas to stabilize barrier islands and when island breaches are filled (Speybroeck et al. 2006, Leewis et al. 2012), as was done on Fire Island following Hurricane Sandy with the Fire Island to Moriches Inlet stabilization project. Due to the federally threatened status of piping plovers, the effect of anthropogenic changes to their prey base needs to be assessed and, where appropriate, mitigated.

Piping plovers, which breed on barrier islands, forage on terrestrial and marine invertebrates by pecking for prey on the surface of sediment, probing shallowly into the substrate, and occasionally by gleaning invertebrates on vegetation (Shaffer and Laporte 1994, Cuthbert et al. 1999, Majka and Shaffer 2008, Cisek 2013). The variety of foraging methods which plovers exhibit means that they likely prey on a diverse range of taxa. The quantity of prey available in habitats can determine habitat

quality and influence piping plover nesting densities (Elias et al. 2000, Cohen et al. 2009). Prey abundance and location can contribute to nest site location, as plovers favor nesting close to moist substrates for availability to food sources during the nesting period (Elias et al. 2000, Cohen et al. 2009). Natal territories with available high-quality foraging habitat can contribute fitness advantages to offspring (Catlin et al. 2014). Specifically, plover chicks with access to high densities of terrestrial invertebrates weigh more, have higher foraging rates, and are more likely to survive (Loefering and Fraser, 1995, Cohen et al. 2009, Catlin et al. 2015). Habitat changes resulting from anthropogenic and natural forces have an effect on plover population dynamics, and changes in prey abundance may contribute to the effect (Cohen et al. 2009, Catlin et al. 2015). Plover prey sampling in the pre-laying season has indicated that benthic prey are more available than terrestrial prey species (Cohen and Fraser 2010). Therefore, determining whether any of the post-Hurricane Sandy habitat alterations support better piping plover prey communities may improve the overall population by suggesting how to create or modify habitat in the future.

Methods

To assess the difference in the mean number of terrestrial invertebrates collected on bay beaches, ocean beaches, and barrier interior, we performed a Kruskal-Wallis chi-squared test using the invertebrate samples from 2014–2019 and 2019 alone (see Part 2, Section 1 for field methods). We used a negative binomial mixed model to predict the mean invertebrate catch over a three-hour period in each of four habitat types (bay intertidal, ephemeral pool, ocean intertidal, island interior) and each of three treatment levels (overwash, breach fill, restoration area) with the combined invertebrate data from 2014–2019. For the grouping variables within the analysis, habitat type (beach, ephemeral pool, and interior) was assigned for each individual invertebrate sample, at the time of data collection. Treatment level was assigned based on the joining of a shapefile of all invertebrate sample locations with shapefiles of the overwashes, breach fills and restoration areas. Results were

extrapolated to three-hour periods to compare to past studies (Houghton 2005, Cohen et al. 2009, Anteau and Sherfy 2010).

Results

During 2014–2019, we collected 2591 invertebrate samples, of which 1305 (50.4%) contained at least one invertebrate. During 2014–2019, there was a significant difference in the number of invertebrates collected among the three different geologic locations of bay beach, barrier interior, and ocean beach (K-W = 233.95, $P < 0.001$; Table 20). Across the whole study, bay beach samples had nearly 4x as many invertebrates caught over the 30-minute sample period. Similarly, in 2019, there was a significant difference in the number of invertebrates collected among the three different geologic locations (K-W = 15.04, $df = 2$, $P < 0.001$). In 2019, invertebrate samples in the bay and ocean beaches in 2019 had a greater mean arthropod catch than barrier interior invertebrate samples, but they did not differ from one another as in the overall dataset (Table 21).

Table 20. Mean number of invertebrates captured during a 30-minute period at bay beach, ocean beach, and barrier interior habitats on Fire Island and Westhampton Island, May through August 2014–2019.

Geologic Location	Mean Arthropods/ 30min	SE	N
Bay Beach	4.10	0.36	537
Barrier Interior	1.06	0.077	1363
Ocean Beach	1.64	0.36	594

Table 21. Mean number of invertebrates captured during a 30-minute period at bay beach, ocean beach, and interior habitats on Fire Island and Westhampton Island, May through August 2019.

Geologic Location	Mean Arthropods/ 30min	SE	N
Bay Beach	3.46	0.87	59
Barrier Interior	1.39	0.31	214
Ocean Beach	3.48	1.89	111

Among habitat types, ephemeral pools and bay beach had greater projected invertebrate catches than the ocean beach or barrier interior. For the treatment types, overwashes had greater invertebrate catches than the restoration areas and the breach fills (Figure 27). Although the invertebrate catch rate was high in ephemeral pools, ephemeral pools were rare, as indicated by the small sample size (Figure 27).

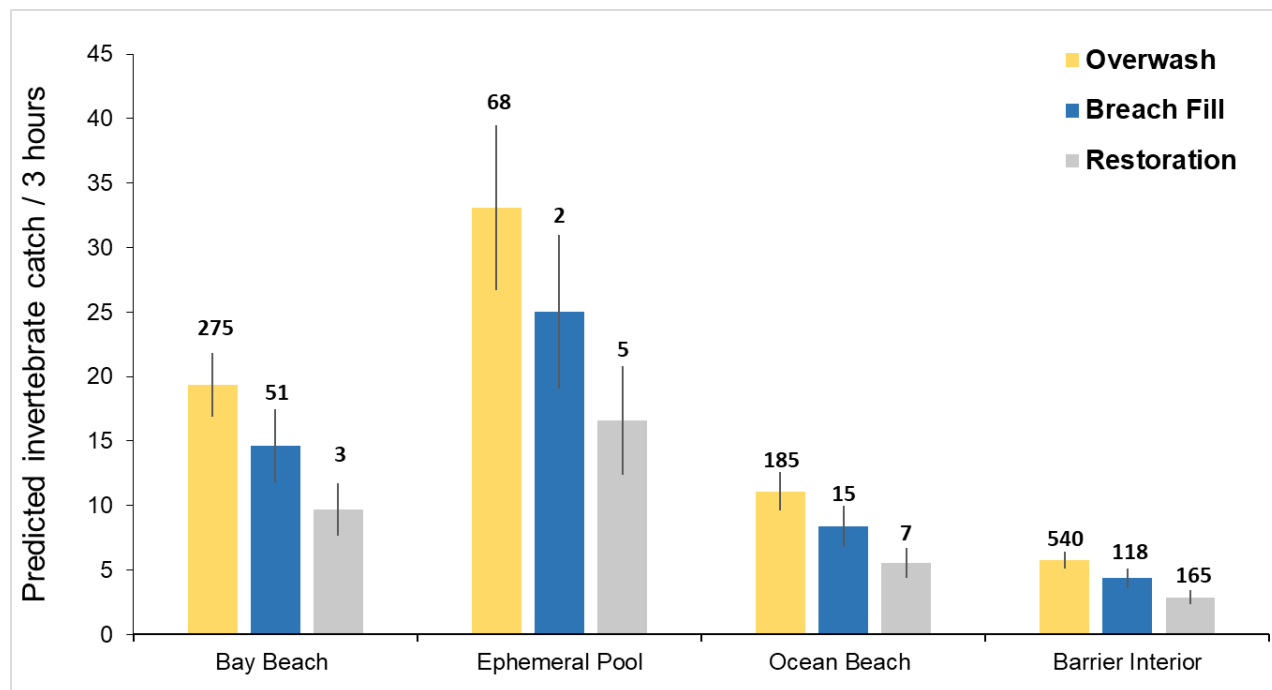


Figure 27. Predicted invertebrates catch over a projected three-hour period in various habitats from 2014–2019. We predicted invertebrate catch using a negative binomial mixed model. Invertebrate samples were collected over 30-minute periods and projected to 3-hours to facilitate comparison to similar piping plover studies. Numbers above bars indicate sample sizes. Error bars represent standard error. Sample sizes differed among habitats because samples were collected in proportion to habitat availability.

Discussion

Understanding the availability of prey resources in relation to bird use is an important piece of assessing habitat quality. From terrestrial invertebrate samples on Fire Island and Cupsogue during 2014–2019, our results indicate what past studies also have indicated, that low-energy moist habitats, such as bay beach and ephemeral pools have higher invertebrate abundance than interior and ocean

intertidal habitats (Loefering and Fraser 1995, Elias et al. 2000). Contrary to some studies, we found that the ocean intertidal habitat was generally more productive than interior habitats (Loefering and Fraser 1995), but invertebrate availability in the intertidal likely varies with slope, elevation, and wrack availability, which we did not evaluate here. This study also indicated that more terrestrial invertebrates were caught in overwashes compared to breach fills and restoration areas.

More invertebrates in the overwashes is particularly interesting, as the largest overwash, Old Inlet East, has overwashed multiple times since Hurricane Sandy, and it might be expected that this would continually disturb the invertebrate community (McCabe and Gotelli 2000). However, substrate invertebrates may be more disturbed by frequent overwashing than terrestrial invertebrates, such as Dipterans and Coleopterans, which can fly and recolonize an area quickly. The restoration areas did not have intertidal areas included in their design polygons, and we only included areas within the design footprint in our evaluation, which likely drove the lower predicted invertebrate abundance there. Future evaluations of the restoration areas should also consider sampling adjacent, accessible inter-tidal zone even if not explicitly in the design criteria.

Overall, understanding which habitats support the greatest invertebrate communities is essential, as greater invertebrate abundance and densities are likely to improve foraging efficiency of both adult plovers and chicks, leading to improved growth rates and potentially higher survival rates (Catlin et al. 2014). Ideally, future habitat construction can improve on the creation of ephemeral pools in design criteria and perhaps mimic overwash dynamics, and allow access to intertidal zones to improve invertebrate abundance for plovers.

Section 7: Quantify the interactions of predators with shorebird nests and chicks

Introduction

Predator disturbance has been shown to increase the probability of nest abandonment (Doherty and Heath 2011), thus, even in areas implementing nest exclosures, predators can cause nest failure through harassment and predation of incubating adults (Roche et al. 2010). Disturbance also can result in a change in behavior due to the perceived risk of predation (Frid and Dill 2002, Swaisgood et al. 2018). In the case of plovers and other shorebirds, disturbance can influence the incubating or brooding behavior of adults and foraging behavior in chicks, both of which can have a negative influence on chick survival (Weston and Elgar 2005, Hillman et al. 2015, DeRose-Wilson 2018). Furthermore, soon after chicks hatch and are mobile, they no longer benefit from the protection of nest exclosures.

Many piping plover (*Chradrius melodus*) nests on the Atlantic Coast of the United States are protected by exclosures designed to inhibit predator access to eggs (Melvin et al. 1992) and nest survival is typically high as a result (Catlin et al. 2015, Cohen et al. 2016). Despite this, it is still vital to understand the factors that influence potential nest and adult disturbance to gain a better perspective on nest protection and disturbance reduction, especially for aerial predators or predators that are small enough to fit through the fencing of nest exclosures (Murphy et al. 2003, Neuman et al. 2004).

Remote cameras are valuable tools for collecting data on wildlife interactions that often are difficult to observe directly (Trollet et al. 2014). Cameras are relatively non-invasive and can collect photo data throughout the day and night, recording interactions that occur when direct observation is difficult or impossible (Murphy et al. 2017, Hunt et al. 2019*b*). The effect of disturbance of humans and predators on wildlife species is well-understood (Gill et al. 1996, Ciuti et al. 2012, Suraci et al. 2019), however, using cameras to capture unobservable wildlife interactions can provide valuable insight into potential opportunities for management to reduce disturbance to threatened species. In this objective, we used remote cameras to quantify the interactions between predators and exclosed

plover nests and to identify potential sources of disturbance to nests and chicks. Although we did not directly assess disturbance in this objective, with the information gathered from our remote cameras, we hoped to gain perspective of the local predator community and other sources of potential disturbance that may be affecting the fate of plover nests and chicks in our study area. Moving forward, this information can help focus management decisions on strategies better designed to protect nests and chicks from disturbance detected by our cameras.

Methods

We installed remote cameras (Reconyx Rapidfire, RC60 Covert IR, Holmen, WI, USA) on nest exclosures in 2016–2019, as early as May 13 and as late as July 7. Cameras were placed on nests of varying age, as we did not place cameras on nests until both incubating adults were captured. Cameras were set to capture one photo every five minutes in addition to capturing three photos in a burst whenever the motion sensor was triggered with a one second cooldown period between bursts. After installing a camera on the outside of an exclosure, we ensured the camera was accepted by the incubating adults using similar methods that managers use to confirm exclosure acceptance. If an adult did not return to incubate within 30 minutes, we removed the camera. We checked camera batteries and SD memory cards opportunistically, often during nest checks to reduce the time spent at a nest, thus the interval between each camera check varied. We removed cameras from exclosures once the nest hatched and the brood left the nest location. Therefore, the time each camera was on an exclosure varied by nest.

We used 30-minute detection periods to analyze the camera data. This allowed us to distinguish between different capture events for non-uniquely identifiable animals. For instance, if a white-tailed deer lacking identifiable features was captured in a photo and then left the frame, any white-tailed deer seen within 30 minutes of the first was assumed to be the same animal unless the two were distinguishable from one another and, thus, would only be counted once. Additionally, if a white-tailed deer remained in the camera frame for 31 minutes, it would count as two separate white-

tailed deer capture events. Individuals detected on camera, but not included in the results, were plovers, plover monitors, and plover monitor vehicles. For more information regarding the interaction between plovers and red fox, see details on use of high frequency GPS collar locations of red foxes during exclosure setup and egg hatching periods in the red fox report section below (Part 3, Section 3).

Results

In 2016, we placed 14 remote nest cameras across the study area. Cameras were present on exclosures between three and 34 days for a total of 238 trap nights ($\bar{x} = 17$, $SE = 2.14$; Table 22). Gulls (*Laridae spp.*), red foxes (*Vulpes vulpes*), and crows (*Corvus spp.*) were the taxa with the most individuals pictured, while red foxes, crows, and toads (*Anaxyrus spp.*) were the taxa with the most capture events. The taxa with the least number of individuals pictured and least number of capture events included a mourning dove (*Zenaida macroura*), a brown thrasher (*Toxostoma rufum*), and a sparrow (*Passeridae sp.*) with one each (Table 23).

In 2017, we placed 27 remote nest cameras across the study area. Cameras were present on exclosures between two and 26 days for a total of 329 trap nights ($\bar{x} = 12.19$, $SE = 1.04$; Table 22). Gulls, humans, and white-tailed deer (*Odocoileus virginianus*) were the taxa with the most individuals pictured, while gulls, humans, and crabs were the taxa with the most capture events. The taxa with the least number of individuals pictured and least number of capture events included an unknown tern (*Sternidae sp.*), a great-horned owl (*Bubo virginianus*), an eastern cottontail (*Sylvilagus floridanus*), a rat (*Rattus sp.*), a black skimmer (*Rynchops niger*), a grackle (*Quiscalus sp.*), and an eastern kingbird (*Tyrannus tyrannus*) with one each (Table 28).

In 2018, we placed 27 remote nest cameras across the study area. Cameras were present on exclosures between one and 40 days for a total of 396 trap nights ($\bar{x} = 14.67$, $SE = 1.69$; Table 22). Humans, unknown terns, and least terns (*Sternula antillarum*) were the taxa with the most individuals pictured, while humans, least terns, and unknown bird spp. were the taxa with the most capture

events. The taxa with the least number of individuals pictured and least number of capture events included an eastern cottontail, a semi-palmated plover (*Charadrius semipalmatus*), and a peregrine falcon (*Falco peregrinus*) with one each (Table 23).

In 2019, we placed 19 remote nest cameras across the entire study area. Cameras were present on exclosures between five and 29 days for a total of 236 trap nights ($\bar{x} = 12.42$, $SE = 1.39$; Table 22). Gulls, humans, and unknown birds were the taxa with the most individuals pictured and the most capture events. The taxa with the least number of individuals pictured and least number of capture events included a mourning dove, a barn swallow (*Hirundo rustica*), a northern mockingbird (*Mimus polyglottos*), a diamondback terrapin (*Malaclemys terrapin*), and an unknown mammal with one each (Table 23).

During 2016–2019, we placed 87 remote nest cameras across the study area. Cameras were present on exclosures between one and 40 days for a total of 1,199 24-hour periods (trap nights; $\bar{x} = 13.78$, $SE = 0.79$; Table 27). When combined, gulls had the most individuals pictured, followed by humans and unknown birds. However, humans had the greatest number of capture events, followed by gulls and unknown birds. When grouped by class, birds had the greatest number of individuals pictured as well as the most capture events followed by humans, non-human mammals, toads, crabs, reptiles, and unknown (Table 24). In 1,199 trap nights, footage confirmed no predation events and only one instance of a potential mammalian predator entering an exclosure. In 2017, a rat, likely a Norway rat (*Rattus norvegicus*) based on a small mammal inventory done on Fire Island in 2002 (USACE 2002), was pictured inside of the exclosure but not depredating the eggs. There were 27 ghost crab capture events at two separate plover nests (*Ocyropsis quadrata*), and in most of the pictures, they were inside of exclosures. Toads, likely Fowler's toads (*Anaxyrus fowleri*), were captured on cameras 68 times throughout the study, and were often inside of exclosures. Examples of photo captures from nest cameras can be found in Figure 28.

Table 22. Number of nest cameras placed in each management unit 2016–2019 and the two taxa with the most individuals pictured and most capture events each year.

Year	Management Unit	# of Cameras	Trap Nights	Taxa with the Most Individuals	Taxa with the Highest Number of Capture Events
2016	Smith Point County Park	2	18	White-tailed Deer (1) Red-winged Blackbird (1)	White-tailed Deer (1) Red-winged Blackbird (1)
	Cupsogue Beach County Park	2	17	Gull sp. (1) Unknown Bird sp. (1) Red-winged Blackbird (1)	Gull sp. (1) Unknown Bird sp. (1) Red-winged Blackbird (1)
	Fire Island National Seashore	6	142	Crow (16) Toad spp. (10)	Crow (19) Toad spp. (10)
	Robert Moses State Park	4	61	Red Fox (19) Gull spp. (19)	Red Fox (19) Toad spp. (5) White-tailed Deer (5)
2017	Smith Point County Park	10	115	White-tailed Deer (20) Gull spp. (3) Raccoon (3)	White-tailed Deer (18) Raccoon (3)
	Cupsogue Beach County Park	3	49	Common Tern (3) Mute Swan (2)	Common Tern (2) ^b
	Fire Island National Seashore	8	83	Least Tern (10) Toad spp. (8)	Least Tern (8) Toad spp. (8)
	Robert Moses State Park	6	82	Gull spp. (391) Human ^a (277)	Gull spp. (90) Human ^a (72)
2018	Smith Point County Park	11	191	Black-bellied Plover (45) Least Tern (35)	Least Tern (30) Unknown Bird spp. (22)
	Cupsogue Beach County Park	4	64	Human ^a (48) Gull spp. (32)	Gull spp. (26) Human ^a (24)
	Fire Island National Seashore	3	51	Least Tern (68) Unknown Bird spp. (53)	Unknown Bird spp. (40) Least Tern (38)
	Robert Moses State Park	9	90	Tern spp. (139) Human ^a (133)	Human ^a (84) Tern spp. (62)

2019	Smith Point County Park	9	104	Unknown Bird (26) Gull spp. (21) Deer (21)	Unknown Bird spp. (19) Toad (19)
	Cupsogue Beach County Park	1	15	Gull spp. (6) ^b	Gull spp. (5) ^b
	Fire Island National Seashore	6	91	Gull spp. (1283) Human ^a (263)	Gull spp. (147) Unknown Bird spp. (102)
	Robert Moses State Park	3	26	Human ^a (983) Gull spp. (228)	Human ^a (190) Gull spp. (34)
	Total	87	1199	-	-

^aOnly non-plover monitor humans were counted ^bFollowed by ≥ 3 different taxa with 1 detection each

Table 23. Number of nest camera capture events per year and subsite, Fire Island and Westhampton Island, 2016–2019. See Table 2 for subsite descriptions.

Year	Subsites of Nest Cameras with Capture Events	Taxa ID	Number of Individuals	Number of Capture Events
2016	DMP, CSE	Gull spp.	24	8
	DMP, OSS	Red fox	19	19
	OIE, BRO	Crow spp.	19	16
	DMP, OSS, OIE	Toad spp.	15	15
	DMP, BRO	White-tailed Deer	14	10
	BRO	Unknown Bird spp.	8	7
	NBE, SPTE, CSW	Red-winged Blackbird	7	6
	DMP, OSS, CSE	Human ^a	6	4
	BRO	Grackle spp.	5	4
	OSS, OIE, BRO	Unknown	3	3
	OSS, OIE	Northern Mockingbird	3	3
	BRO	Raccoon	2	2
	BRO	Willet	2	2
	BRO	Mourning Dove	1	1
	OIE	Brown Thrasher	1	1
	BRO	Sparrow sp.	1	1
2017	DMP, OSS, FLD4, SPTE, CSW	Gull spp.	394	92

	DMP, OSS, FLD3, FLD4	Human ^a	273	71
	DMP, OSS, STP, FLD4, OIE, SPTE	White-tailed Deer	28	26
	OSS, DMP	Crab spp.	27	27
	DMP, OIE, NBW	Toad spp.	11	11
	OIE	Least Tern	10	8
	DMP, OSS, STP, FLD4, NMA	Red fox	9	9
	DMP	American oystercatcher	8	6
	DMP, STP, CSE	Crow spp.	6	6
	OIE, NMA, SPTE	Raccoon	5	5
	OIE, SPTE	Willet	4	3
	FLD4, CSW	Unknown Bird spp.	3	3
	CSW	Common Tern	3	2
	OIE, CSW	Red-winged Blackbird	2	2
	CSW	Mute Swan	2	1
	DMP	Tern sp.	1	1
	BRO	Great-horned Owl	1	1
	CSE	Eastern Cottontail	1	1
	CSW	Rat sp.	1	1
	DMP	Black Skimmer	1	1
	PSO	Unknown Grackle sp.	1	1
	OIE	Eastern Kingbird	1	1
2018	DMP, OSS, STP, FLD3, FLD4, OIE, BRO, PSO, SPTE, CSW, CSE	Human ^a	204	122
	DMP, OIE, NBW, SPTE, CSW, CSE	Tern spp.	165	81
	DMP, OIE, SPTE, CSW, CSE	Least tern	144	98
	DMP, FLD4, OIE, BRO, PSO, NBW, SPTE, CSW, CSE	Unknown Bird spp.	126	92
	DMP, FLD4, OIE, BRO, PSO, NBW, SPTE, CSW, CSE	Gull spp.	79	58
	DMP, FLD4, BRO, PSO, NBW, SPTE	White-tailed Deer	49	39
	SPTE	Black-bellied Plover	45	4
	OIE, BRO, PSO, SPTE	Toad spp.	17	15
	DMP, BRO, NBW, CSW, CSE	American Oystercatcher	11	7
	DMP	Common Tern	10	5

	SPTE	Snowy owl	9	9
	CSW, BRO	Red-winged Blackbird	8	8
	OIE, PSO	Willet	4	4
	PSO	Mourning Dove	4	3
	PSO, CSW	Unknown	4	3
	CSW, CSE	Dog	3	3
	OIE, STP	Crow spp.	3	3
	FLD4	Red fox	2	2
	PSO	Northern Mockingbird	2	2
	BRO, NBW	Grackle spp.	2	2
	CSE	Eastern Cottontail	1	1
	SPTE	Semi-palmated plover	1	1
	BRO, NBW	Peregrine Falcon	1	1
	STP, FLD3, OIWR, OIW, OIE, NBW, SPTW, SPTE, CSE	Gull spp.	1539	204
	OSS, STP, FLD3, OIWR, OIW, OIE, SPTE, CSE	Human ^a	1218	267
	OIWR, OIW, OIE, SPTE, CSE	Unknown Bird spp.	189	122
	STP, FLD3, OIWR, OIW, SPTE, NBW, NBE, CSW, CSE	White-tailed Deer	61	44
	DMP, OIWR, OIW, NBW, SPTW, SPTE	Toad spp.	25	25
	OIWR, OIW, NBW	Least tern	19	14
	FLD3, OIWR, NBW, SPTE	American Oystercatcher	9	6
2019	OIW, NBW	Unknown Grackle spp.	8	7
	OIWR	Glossy Ibis	7	4
	SPTE	Unknown	6	6
	SPTE	Black-bellied Plover	6	2
	FLD3, FIL, OIE	Dog	5	5
	OIW, OIWR	Crow spp.	5	5
	CSE	Red-winged Blackbird	4	3
	OIWR	Mute Swan	4	3
	OIWR	Sparrow spp.	2	2
	OIWR	Unknown Tern spp.	2	2

OIWR	Canada Goose	2	1
SPTE	Mourning Dove	1	1
OIWR	Barn Swallow	1	1
CSE	Northern Mockingbird	1	1
OIWR	Unknown Mammal sp.	1	1
OIWR	Diamondback Terrapin	1	1

^a Only non-plover monitor humans were counted.

Table 24. Cumulative capture events from 2016–2019 grouped by class.

Class	Taxa	Number of Individuals	Number of Capture Events	Total Number of Individuals	Total Number of Capture Events
Mammalia	Human ^a	1701	464	1701	464
	White-tailed Deer	152	119		
	Red Fox	30	30		
	Dog	8	8		
	Raccoon	7	7	201	168
	Eastern Cottontail	2	2		
	Unknown Mammal sp.	1	1		
	Rat sp.	1	1		
	Gull spp.	2036	362		
	Unknown Bird spp.	326	224		
Aves	Least Tern	173	120		
	Tern spp.	168	84		
	Black-bellied Plover	51	6		
	Crow spp.	33	30		
	American Oystercatcher	28	19		
	Red-winged Blackbird	21	19		
	Grackle spp.	16	14		
	Common Tern	13	7		
	Willet	10	9		
	Snowy Owl	9	9	2921	933
	Glossy Ibis	7	4		
	Northern Mockingbird	6	6		
	Mourning Dove	6	5		
	Mute Swan	6	4		
	Sparrow spp.	3	3		
	Canada Goose	2	1		
	Brown Thrasher	1	1		
	Semi-palmated Plover	1	1		
	Barn Swallow	1	1		
	Peregrine Falcon	1	1		
	Great-horned Owl	1	1		
	Black Skimmer	1	1		

	Eastern Kingbird	1	1		
Malacostraca	Crab spp.	27	27	27	27
Amphibia	Toad spp.	68	66	68	66
Reptilia	Diamondback Terrapin	1	1	1	1
Unknown	Unknown	13	12	13	12

^aOnly non-plover monitor humans were counted





Figure 28. Examples of captures from nest cameras. Species pictured include red fox, crow sp., snowy owl, raccoon, peregrine falcon, rat sp., and great horned owl.

Discussion

Remote cameras we placed on plover nests detected both predator and non-predator species at nest exclosures. Gulls, humans, unknown or unidentifiable birds, and least terns had the most capture events and were the taxa with the most individuals pictured at exclosures across all years.

When capture events were considered by class, birds were the most commonly pictured, suggesting that their prevalence in our study system may have an effect on nests and chicks if the number of individuals pictured is correlated with depredation or changes in plover behavior. There were nearly 6 times as many bird capture events as there were non-human mammal capture events, but 254 (27%) of the identifiable bird capture events (semi-palmated plover, barn swallow, black skimmer, mourning dove, willet, northern mockingbird, tern spp., etc.) were of species that likely pose little to no threat to plover nests or chicks apart from the potential negative effects of interspecific agonistic behavior exhibited by adults towards individuals within close proximity to their nest or brood (Maxson 2000). However, gulls, crows, grackles, owls, peregrine falcons, and red-winged blackbirds (*Agelaius phoeniceus*) are all known predators of piping plover nests or chicks (Lauro and Tanacredi 2002, Ivan and Murphy 2005). American oystercatchers also pose a threat to nests as they have been observed removing eggs and killing plover chicks (Lauro and Tanacredi 2002). Many 'unknown' birds detected were unidentifiable due to poor photo quality or lighting, and sometimes were at unknown distances from the camera, resulting in a lack of perspective. These unknown bird

capture events likely included some potential predators, such as crows and grackles. However, even if we assume that all unknown birds were non-plover predators, 49% of capture events and 73% of all individual birds pictured would still be known plover predators. In fact, gulls were the greatest non-human source of potential disturbance captured on our nest cameras. The amount of avian presence we detected at nest exclosures suggests that birds may play an important role in nest disturbance. If presence near nest exclosures during incubation is also an indicator of future interactions with broods, avian predators with many capture events, such as gulls, may also be substantial sources of chick predation or disturbance.

During the 2018 and 2019 field seasons, we observed peregrine falcons during plover surveys, sometimes perched on nest exclosures and hunting shorebirds in the area. On one occasion, plover monitors observed a peregrine falcon dive in the direction of an adult plover, but instead, capture a nearby least tern (*Sternula antillarum*) fledgling. In 2019, a peregrine falcon was seen eating a plover chick while on its associated nest's exclosure and the flag leg of an adult from a different nest was found at the base of the same exclosure less than a week later. In 2018, we captured photos of a peregrine falcon on a nest camera less than an hour before the carcass of one of the incubating adults was found inside the same exclosure. Given how often we observed peregrine falcons on or near exclosures while surveying, we expected more peregrine falcon capture events than what our cameras recorded. Owls, such as the great horned owl, also are known predators of plovers and their range encompasses our study area year-round (Catlin et al. 2011*a*). Only one great-horned owl was captured on our cameras in all years of this study. However, in 2017, we confirmed a great-horned owl as the source of mortality for a fledgling at Old Inlet East. Further, in 2019, we discovered owl feathers on at least two exclosures and large owl tracks in the sand outside of exclosures that were surrounded by unidentified shorebird feathers, suggesting that owls may also have been hunting from exclosures like peregrine falcons. Interestingly, a snowy owl was observed near exclosures at Smith Point in late May 2018. Most snowy owls have departed for the breeding grounds by the time plovers in our study area begin to initiate nests in mid to late April (Holt et al. 2015), so it is unlikely that snowy owls present

much of a disturbance or source of predation to plovers in our study area. Being at ground level, our cameras were not in the ideal position to capture all interactions between raptors and plover nests. Since larger aerial predators likely perch higher than our cameras' field of vision on the top of exclosures, more often than they walk along the ground, their presence in this system likely is being underrepresented by our camera data. In contrast, gulls may be more likely to be detected by our cameras due to their propensity for walking or roosting on the ground.

Although detected at a lower rate, mammals also contributed to the potential disturbance of plover nests in our study area. Most mammal capture events came from white-tailed deer, and while deer have been known to trample nests and consume eggs or even live birds (Pietz and Granfors 2000, Ivan and Murphy 2005), they likely do not present much of a threat to plovers in our study area given that we never observed nest failure in association with deer sign. However, red foxes were the second most detected mammal and were recorded on cameras in every year except 2019. Capture events of red foxes on our cameras decreased each year following 2016, which tracks with the timeline of the mange outbreak (Part 3, Section 1). If these nest capture events were correlated with actual numbers of red foxes, the potential disturbance from red foxes on plover nests decreased substantially along with the red fox population decline. In 2018, our cameras recorded a red fox at exclosures twice, suggesting that even at very low numbers, red foxes can contribute to nest disturbance and, as known predators of plovers, play a role in the fate of nests and chicks. Although a rat was only present during one capture event, they are known plover nest predators (Lauro and Tanacredi 2002), therefore, their presence at nests, and their ability to enter an exclosure, poses a threat of nest disturbance and egg loss.

Toads and ghost crabs were the taxa most commonly seen inside of nest exclosures. Although toads do not pose a threat to nesting plovers, ghost crabs depredate eggs (Kwon et al. 2018). In 2019, an adult plover was found decapitated in a ghost crab burrow at Watch Hill and though we do not believe the adult was killed by a ghost crab, they have been observed taking chicks in Maryland and at Cape Hatteras National Seashore in North Carolina (Loeagering and Fraser 1995, Kwon et al. 2018).

In this study, at both nests where ghost crabs were pictured, they were seen entering burrows within or very close to the nest enclosure. Being small enough to enter enclosures, ghost crabs are one of the potential predators in our study area that could affect the survival rate of enclosed nests if they were present in greater numbers (Kwon et al. 2018).

Human disturbance has been observed to have a negative effect on plover chick survival, foraging rate, and body condition (DeRose-Wilson 2018). Predator and human disturbance also have been linked to an increased risk of nest abandonment in piping plovers (Doherty and Heath 2011). Furthermore, evidence from multiple studies suggests that birds may respond similarly to humans as they would to other predators (Frid and Dill 2002, Beale and Monaghan 2004). Given the deleterious effects of disturbance on plover nests and chicks, these findings are important to consider moving forward (Hunt et al. 2018*b*). Not only must plovers be wary of myriad potential predators within this system, but they also must contend with a near constant presence of human activity in some areas at certain times of the breeding season. Despite the use of symbolic fencing, non-plover monitor humans were in the top two contributors to capture events and individuals pictured in all years except 2016. Although we were unable to assess human disturbance on plovers based purely on the number of capture events, we can make some inferences based on the photo data. Many capture events showed humans recreating between the nests and important foraging habitat such as wrack and low-energy intertidal habitat (Loefering and Fraser 1995), effectively blocking any chicks from reaching them. During June–August, when beach recreation is at its highest, chicks are likely forced to avoid these preferred foraging habitats, especially on the weekends, and exert more energy foraging in less optimal habitat, such as interior, to avoid people on the shore (DeRose-Wilson 2018). Other capture events showed humans disregarding symbolic fencing and directly approaching nest enclosures. Humans may also be directly affecting incubating adult behavior if nests are close enough to these heavily trafficked areas or if humans disregard symbolic fencing protections. In the future, assessing human disturbance and its effects on the incubating behavior of piping plover in our study area

would provide valuable insight into the management of recreational activities near protected nesting areas and any potential limitations of symbolic fencing buffers (Weithman 2019).

The detected predator community varied annually within our study area and understanding how to adapt management strategies to account for such a dynamic system is vital. There was a significant avian predator presence in the study area, and managers should consider the implications of these findings when deciding to exclose nests and for how long to leave exclosures up following hatch. Raptors have been known to adapt their hunting strategies with the introduction of artificial perches or by cuing in on nests (Reinert 1984, Niehaus et al. 2004, Murphy et al. 2003), and if exclosures are being used as eating or hunting perches in our study area, leaving them up after hatch may be detrimental to plovers in the area. Additionally, there is a potential for the red fox population to recover in our study area and recommence exerting predatory pressures on the plover population dynamics (Part 2, Section 4). It is crucial to continue monitoring predators via nest cameras as the community changes in the following years and, ultimately, how these changes may influence the plover population in the future. Finally, using our cameras to assess disturbance to plovers by linking behavioral changes of the incubating adult to capture events could lead to a better understanding of the indirect effects that predators, non-predators, and humans have on the plovers in our study area (Hillman et al. 2015, DeRose-Wilson et al. 2015).

Part 3: Red Fox Monitoring on Fire Island, New York

Section 1: Red Fox Movements, Habitat Selection, and Demography on Fire Island, New York

Objective 1: Quantify the abundance and occupancy of red foxes and relate these parameters to changes in habitat and predator management activities

Objective 2: Estimate red fox reproductive success and adult survival, and variation in these population parameters, related to habitat composition and predator management

New Objective (to begin post-COVID restrictions) 1: Produce an index of fox abundance to understand the recovery rate of the fox population.

New Objective (to begin post-COVID restrictions) 2: Estimate red fox reproductive success and relate it to population growth during the recovery from the mange outbreak.

Introduction

Information on population size and the factors influencing animal abundance is needed for wildlife management and conservation. For threatened and endangered species conservation, information on the population ecology of both the target species and its important predators can help guide recovery efforts. In June 2015, we began monitoring a coastal red fox population as part of a study investigating red fox interactions with the federally threatened piping plover (*Charadrius melodus*). Red foxes are key predators of the federally threatened piping plover (*Charadrius melodus*) along the North American Atlantic coast, leading to frequent red fox management efforts aimed at reducing predation on these and other shorebirds (Hunt et al. 2019a). Shortly after the start of data collection, a series of sarcoptic mange outbreaks began in the study area, presenting an unexpected opportunity to examine the effects of sarcoptic mange on red fox population dynamics in a North American coastal ecosystem.

Sarcoptic mange has been identified as a driver of red fox population dynamics in several parts of the world. In Bristol, UK, red fox population density decreased by >95% following an outbreak

(Baker et al. 2000). Similar declines in red fox populations following mange outbreaks were reported in Sweden (Lindström et al. 1994) and Spain (Gortázar et al. 1998). However, there is less information on the effects of sarcoptic mange in North American red fox populations, with much of the published literature about mange in red foxes coming from European studies (Niedringhaus et al. 2019). In the United States, Gosselink et al. (2007) reported lower survival of juvenile foxes during times when mange was present versus absent in Illinois red fox populations. Gosselink et al. (2007) also observed differing effects of mange in urban versus rural areas, with mange accounting for 45% of urban red fox mortalities but only 2% of rural red fox mortalities, potentially due to higher densities, increased social interactions, and fewer den sites in urban versus rural areas (Gosselink et al. 2007). Storm et al. (1976) described mange in red foxes in the midwestern United States, but reported that mange did not appear to be limiting red fox numbers in their study area, as other mortality causes were observed more frequently. Aside from these studies, detailed descriptions of mange in red fox populations in North America are relatively limited, and do not address red fox populations in coastal settings.

When considered as a proxy for lethal removal, the effects of such a disease-induced red fox population decline may help inform predator management for shorebird conservation. Here we quantify the impacts of a series of sarcoptic mange outbreaks on red fox population ecology on Fire Island, New York. We estimated trap success, occupancy, minimum abundance and population density, annual reproduction, and survival/mortality rates for red foxes on the island and compared these population parameters before versus during and after mange outbreaks.

Methods

Field methods

Fox capture, ear tagging, and GPS collaring

During August–December 2015, April–May 2016, and February–April 2017 and 2018, we attempted to capture a portion of the red fox population in each study site using padded and offset foothold traps and box traps, following the Association of Fish and Wildlife Agencies' best

management practices (AFWA 2014). Upon capture, we manually restrained red foxes, determined their sex, and ear-tagged them when allowed by site managers. We placed a single tag in the animal's right ear using serially-numbered plastic livestock ear tags (custom MiniTags, Premier 1 Supplies, Washington, IA) at Robert Moses State Park and Smith Point County Park, and small metal ear tags (self-piercing small animal ear tags, size 4; National Band and Tag Company, Newport, KY) at Fire Island National Seashore. The colored plastic ear tags were intended to aid in identification of individual red foxes in remote camera photos and those encountered during transect surveys (see below). In contrast, the small metal ear tags were not intended to be visible in remote camera photos or during transect surveys, but were meant to assist in identifying any individuals recaptured in future years. We also outfitted a sample of red foxes in each site with GPS collars.

GPS tracking

The GPS collars (Quantum 4000E, medium size; Telemetry Solutions, Concord, CA) included a VHF transmitter as well as remote data download and reprogramming capabilities via a UHF connection. To download GPS location data, we used VHF radio telemetry to relocate GPS-collared red foxes every 10-14 days until the programmed drop off date 5-6 months later, or until the animal's death. During these relocations, we also checked for mortality signals, and used VHF signals to locate the remains of red foxes that had died. For those foxes, we attempted to determine a cause of death through close inspection of remains and collected tissue samples, when possible, for later genetic analysis. GPS data from collared red foxes assisted in identifying den locations and in tracking a subset of individuals over time to estimate survival rates. Planned GPS tracking periods spanned August 2015–April 2016, and from February–August of 2016–2018.

Transect surveys for dens, scats, and sign

We established 96 walking transects spanning our 3 study sites to guide den, scat, and sign surveys. We used a 300-m grid overlay to space transects ~300m from each other following a general

north-south direction across the island (Figure 29, Figure 30). These transects ran from the ocean high tide line through all possible habitats to the bayside high tide line, or the point where bayside transects became impassible due to deep marsh or dense shrub thickets. We walked each transect across the island approximately once per month in May–July and October/November–January/February in 2016–2018, ending in February 2019, for a minimum of 3 complete surveys during each spring/summer and fall/winter survey period for each year. These months were chosen to fall within with the piping plover breeding and red fox denning and kit-rearing seasons (May, June, July) and outside of them (October–February).

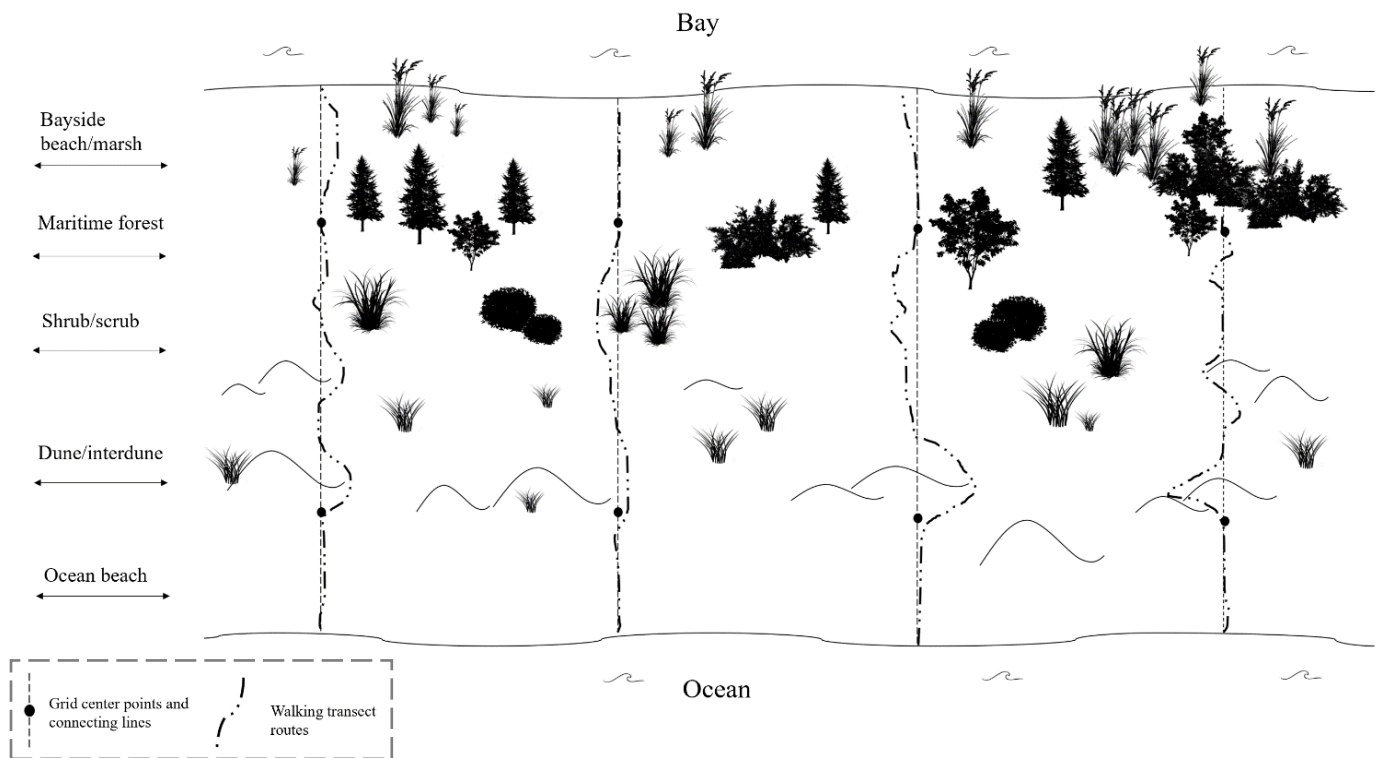
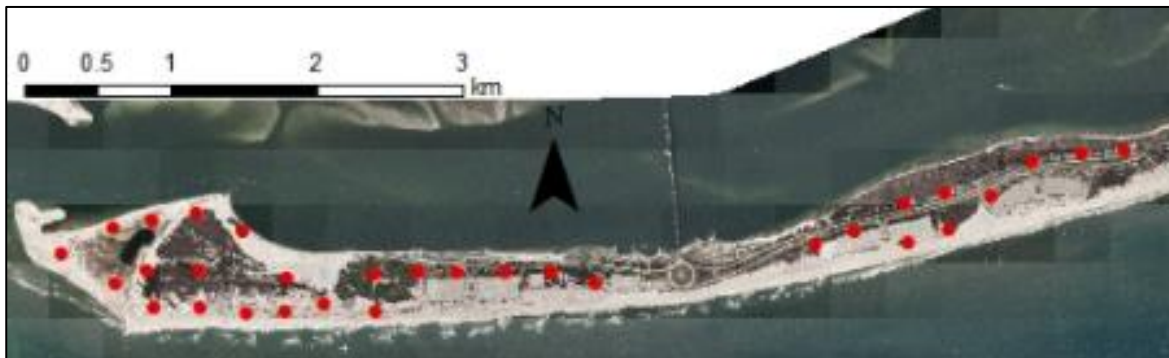


Figure 29. Diagram illustrating habitat types and transect surveys conducted on Fire Island, New York in 2015–2019. We followed game trails, edges, and other likely wildlife travelways along general north-south transect lines based on a 300-m grid overlay of the island. These transects spanned all passable habitat types within each 300-m section of the study area.

During these transect surveys, we followed game trails, habitat edges, and other likely wildlife travelways along the guiding north-south transect lines and searched for red fox dens, scats, tracks,

and other signs of red fox use. We recorded GPS waypoints for all dens and scats found, and all red foxes encountered during surveys. We collected all potential red fox scats found that appeared to be ≤ 1 month old, based on visible biodegradation of fecal material, in a paper bag. We recorded the age (adult or kit), and ear tag color and number (if one was visible) for all red foxes encountered during surveys. For all den sites, we recorded signs of recent use, such as tracks leading in and out of den entrances, scats and prey items in the vicinity, or red foxes observed nearby. In 2017 and 2018, we conducted additional transect surveys in late April/early May to locate breeding dens. During these surveys, multiple observers worked together to search all accessible areas for potential dens, in addition to searching along the game trails and transect areas typically surveyed during other months.



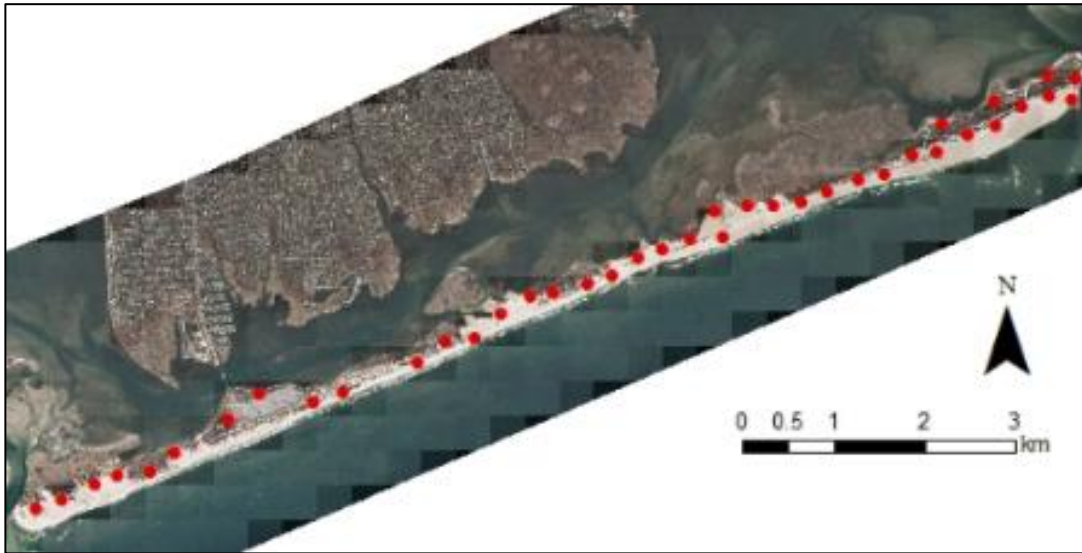


Figure 30. Approximate camera station locations (red dots) at Robert Moses State Park (top), in the Western Wilderness (middle), and Smith Point County Park + Old Inlet East (bottom) on Fire Island, New York in 2015–2019. Remote camera surveys were conducted in September–February of each year, ending in February 2019. Exact locations and numbers of stations varied slightly among years due to changes in habitat that altered site suitability for camera set-up.

Near the end of the study period, from October 2018–February 2019, we conducted monthly driving transect surveys along the main access road and outer beach between Kismet and Watch Hill. During these surveys, we recorded the GPS locations of all red fox tracks and live red foxes encountered along the survey route. We also solicited information on red fox sightings on the island, particularly in the villages in this area, from local National Park Service (NPS) staff and project collaborators.

Den monitoring

We monitored all apparently active red fox dens from the time of discovery until at least 2 weeks after the last signs of active den use. Any newly discovered active dens were revisited within 1 week of discovery and re-assessed to determine the likelihood of current use based on tracks and other sign. Dens that appeared active during this second assessment were added to our ongoing den

monitoring. We visited active dens once every 2 weeks and recorded signs of den use, including fresh tracks, scats, prey remains in the vicinity since the last visit, and any adult red foxes and kits observed in the area. We collected all scats found outside of active dens. Where surrounding habitat provided sufficient cover and human use was low enough to minimize the likelihood of drawing undue attention to dens, we also set up one or more remote cameras (Moultrie M880i, EBSCO Industries, Calera, AL) aimed at den entrances and/or adjacent clearings to determine the number of kits associated with each den. We changed memory cards and batteries and adjusted camera orientation during den monitoring visits.

Remote camera grids

In late September–January/February of 2015–2018, ending in February 2019, we used remote camera grids to survey for red foxes in each of the 3 study sites. We used the same 300-m grid cells and center points that we used to guide our transect surveys to guide remote camera placement, and we established an unbaited camera station within 50 m of the center point of each grid cell containing suitable sites. To minimize the risk of equipment damage and theft, we avoided setting cameras out on the open beach, in low-lying areas prone to flooding, and in areas of heavy human use. For similar reasons, we also excluded grid cells that were entirely composed of large parking lots and inundated marsh.

Each camera station consisted of 2 trail cameras (Moultrie M880c and M880i Gen2, EBSCO Industries, Calera, AL), each mounted on a plastic t-post and facing towards a game trail, clearing, or other potential wildlife travelway. We set cameras on opposite sides of the animal trail to photograph both sides of passing animals. Cameras were programmed to take 3 pictures per trigger, with a 5 second delay after each trigger. We returned every 10–14 days to switch memory cards, replace batteries as needed, and clear any vegetation growing directly in front of the camera. In years following the initial 2015 camera surveys, we set up each camera station in the same location used in previous years, or as close to it as possible if the previous year's location was no longer suitable. Thus,

the exact locations and numbers of camera stations in each grid varied slightly among years due to habitat changes (Figure 30). Each grid was operational for a minimum of 1200 trap nights each year, defined as the number of camera stations multiplied by the number of nights that at least one of the two cameras at each station were in operation.

Lab methods

Scat samples collected during transect surveys and opportunistically during den monitoring and trapping were individually bagged and stored in a 0° C freezer, then transported to a -20° C walk-in freezer for storage until DNA subsampling. For each sample, we separated a small portion (approximately 2ml) of fecal material from the outside edges and tapered ends and submerged this portion in 95% ethanol for DNA preservation. These preserved subsamples were sent to the University of California, Davis Mammalian Ecology and Conservation Unit (MECU) for genetic analyses, including mitochondrial DNA sequencing to verify the source species (Aubry et al. 2009, Miles et al. 2015) and microsatellite genotyping for individual identification (Sacks et al. 2010, 2011, Quinn et al. 2019). Tissue samples collected from dead red foxes were also sent for individual identification via microsatellite genotyping, to determine whether any GPS-collared foxes had been previously detected via scat sampling.

Analytical methods

Trap success

We used photographic detection data from our fall camera grids to calculate red fox trap success as an index of red fox activity for each site and survey period. We calculated trap success as the number of independent red fox detection events divided by the total number of trap nights during which cameras were operational, multiplied by 100 (Kelly and Holub 2008). We used 30-minute detection periods to separate consecutive photographs of red foxes that were not individually identifiable into detection events, so that any red fox photographed within 30 minutes of a previous

series of red fox photographs was counted as a single detection event rather than a separate detection event.

We used a Kruskal-Wallis test to compare red fox trap success before versus during and after mange outbreaks. For these and further comparisons described below, we used the following classifications to group data relative to mange outbreaks: "Before outbreak," for data collected prior to the first observation of signs of mange in a red fox at a given site; "during outbreak," if signs of mange observed in one or more red foxes at a given site during the data collection period; and "after outbreak," for data collected following the last observation of signs of mange in a red fox at a given site.

Occupancy

We used photographic detection data to estimate occupancy (ψ ; i.e., the probability that a randomly selected camera station in a given site is occupied by red fox) and detection probability (p ; i.e., the probability of detecting a red fox at a given camera station during a given survey period, provided it is present in the area; MacKenzie et al. 2002). We used a single species, single season framework in Program PRESENCE (Version 2.12.21, Hines 2006). We did not collapse data, but rather each day was counted as a survey period. Thus, our estimated occupancy relates to the whole survey period, while detection rates are interpreted as detection probability for each day. Because naïve occupancy estimates (i.e. the proportion of camera stations with at least one red fox detection, without accounting for imperfect detection) were already at or close to 1 for so many sites and seasons, we chose not to examine any covariates of occupancy. Instead, we compared the null model and survey-specific detection probability models to determine whether detection probability was best modeled as a constant, or varying by day. We used Akaike's Information Criterion to select the model that best fit the observed data and a cut-off of 4 Δ AIC to identify top models (Burnham and Anderson 2007, Arnold 2010).

Reproduction

We used a combination of remote camera photos, direct observations during den monitoring visits, and GPS collaring data from breeding red foxes to determine the number of adults and kits associated with each den and, when possible, to identify likely breeding groups and to track den relocations over time. We used the maximum number of kits observed at any given point at a breeding group's den, minus any kits known to have died during the den monitoring period, to estimate the number of kits per breeding group that survived through the end of the kit-rearing period, using August 1 as a cutoff for each year. Because these estimates are based on remote camera detections and field-based observations after kit emergence from the den, they do not include any kits that failed to emerge from the den. The numbers of breeding groups presented here are a conservative estimate, as we could not determine whether some breeding dens belonged to a known breeding group or an additional, previously uncounted breeding group. We used a Kruskal-Wallis test to compare litter sizes before versus during and after mange outbreaks.

Survival/mortality

We used known survival or mortality of GPS-collared and ear-tagged red foxes to estimate seasonal adult survival rates for each GPS-tracking period. We used Pearson's chi-square tests for equal proportions to test whether survival differed during periods before versus during and after the mange outbreaks, with the null hypothesis that the proportion of red foxes surviving to the end of the tracking period (exact end dates varied by site, year, and collar deployment date: 31 January–11 April in 2015, August 10–31 in 2016–2018) was equivalent regardless of timing relative to mange. We also used microsatellite genotyping results to estimate the probability that an individual red fox detected in one year would be detected during the following year.

Minimum red fox abundance and density estimates

We combined information from our various data collection methods to estimate the minimum number of red foxes present at each site in 1 February–1 August of 2016–2018. This August cut-off

aligned with the end of our GPS tracking and den monitoring periods for each year, prior to typical red fox dispersal season in our study area. We estimated minimum known red fox abundance during this census period by adding together: 1) the number of GPS-collared red foxes monitored during the GPS tracking period, 2) the number of additional red foxes ear-tagged during a given year's trapping efforts, 3) the number of adults associated with each breeding group (if not included in counts of collared and ear-tagged foxes), 4) the number of kits associated with each breeding group, and 5) any other uniquely identifiable individuals observed during the 1 February–1 August census period (e.g. ear-tagged red foxes from previous years that were seen during transect surveys). When adults associated with a breeding den were not individually identifiable, we assumed a minimum of 2 attending adults in our estimates of minimum population size, and thus added a second adult at dens in which only one adult was seen or photographed at a time. We conservatively included red foxes that were observed during this census period (1 February –1 August) but later found dead in these minimum abundance estimates. We then divided our combined minimum abundance estimates for adults and kits by the area of each study site to estimate minimum densities for each study site and year. Study site areas were calculated using detailed shapefile outlines of each study site based on aerial imagery (flown in April 2016) and the "Calculate Geometry" tool in ArcMap. We used a Kruskal-Wallis test to compare minimum red fox density before versus during and after mange outbreaks, with the null hypothesis that density did not differ with timing relative to mange outbreaks. For these analyses, we considered the density for each site-year combination (i.e. Western Wilderness in 2017) to be a separate sample. We also used the microsatellite genotyping results from genetic analysis of scat and tissue samples to independently estimate the minimum number of red foxes detected in a given year from the transect scat sampling.

Results

Mange outbreaks

Sarcoptic mange was first observed in red foxes in early fall of 2015 east of Old Inlet, and first documented in a photograph that was taken by a visitor at Smith Point County Park, that was shared with us by local collaborators on 3 September 2015. We determined that the red fox in this photograph was exhibiting moderate-severe signs of mange (Figure 31). Prior to that, we had not observed any red foxes with hair loss, facial crusting, skin lesions, or other signs of sarcoptic mange during shorebird monitoring activities conducted in the study area in 2013 and 2014 and a pilot red fox study conducted in June–August 2015 (Audrey DeRose-Wilson personal communication). We first observed signs of mange in a red fox at Robert Moses State Park on 22 May 2017, signaling the beginning of a second outbreak on the island, this time west of Old Inlet. The first observed signs of mange at the Western Wilderness study site were recorded in remote camera photos of a red fox taken there on 18 October 2017.

Fox capture, ear tagging, and GPS collaring

We captured and ear-tagged 41 red foxes between 2015 and 2018, and outfitted 33 of these red foxes with GPS collars (Table 26), including 2 foxes that were recaptured and GPS-collared in multiple years for a total of 35 GPS location datasets. GPS collars that did not allow us to track survival during the tracking period (due to collar malfunctions or inability to relocate after deployment) are not included in this count. We were unsuccessful in capturing any red foxes east of Old Inlet after the 2015 trapping period.

Category and criteria	Sample photo
<u>No signs of mange:</u> No hair loss or skin crusting visible. Any visible lesions appear to be minor cuts or scars.	
<u>Mild signs of mange:</u> Hair loss, skin crusting, and/or lesions limited to one or two small areas of the body.	
<u>Moderate signs of mange:</u> Hair loss, skin crusting, and/or lesions on multiple areas of the body. Hair loss on tail often results in a “whip-like” appearance.	
<u>Severe signs of mange:</u> Hair loss, skin crusting, and/or lesions on large areas of the body. Hair loss on tail often results in a “whip-like” appearance.	

Figure 31. Visual classification scale used to describe the severity of sarcoptic mange symptoms in red foxes during monitoring activities conducted in 2015–2019 on Fire Island, New York.

Table 25. Number of red foxes GPS-collared and ear-tagged by site during each tracking period from 2015-2018 on Fire Island, NY. GPS collar tracking periods spanned August 2015–March 2016, April–August 2016, and February–August 2017 and 2018. GPS collars that did not allow us to track survival during the tracking period (due to collar malfunctions or inability to relocate after deployment) are not included in this table. ♂ = male, ♀ = female.

		2015		2016		2017		2018		Total
Site		♂	♀	♂	♀	♂	♀	♂	♀	
Robert Moses State Park + Lighthouse	GPS collars	2	3	4	2	4	4	1	1	21
	Ear tags	4	5	4	2	4	3	1	2	25
Tract	GPS collars	2	0	2	3	1	3	0	0	11
	Ear tags	0	0	3	3	2	5	0	0	13
Western Wilderness	GPS collars	2	1	0	0	0	0	0	0	3
	Ear tags	1	2	0	0	0	0	0	0	3
Smith Point County Park + Old Inlet East	GPS collars	2	1	0	0	0	0	0	0	3
	Ear tags	1	2	0	0	0	0	0	0	3

Trap success and occupancy

Camera trap success varied among periods (before, during and after the outbreak, Kruskal-Wallis test, $\chi^2_2 = 8.43$, $P = 0.01$; Figure 32). Trap success before mange outbreaks was higher than trap success after the outbreaks (post-hoc Dunn test, $Z = -2.87$, single-tailed $P < 0.01$).

At Smith Point County Park and Old Inlet East, red fox trap success was highest in 2015 as the first outbreak there was ongoing (13.99 red fox detections/100 trap nights), dropped to zero the following year, and remained low through the remainder of the study (3.54 red fox detections/100 trap nights in 2017 and 5.08 red fox detections/100 trap nights 2018). Mange was first detected at Robert Moses State Park between our 2016 and 2017 surveys. Red fox trap success at this site

decreased by 80% from 2016 to 2017 (119.95 red fox detections/100 trap nights in 2016, 18.36 red fox detections/100 trap nights in 2017). Mange was first detected in the Western Wilderness during our 2017 camera surveys. At this site, red fox trap success decreased somewhat in 2017 compared to 2016 (72.62 red fox detections/100 trap nights in 2017 versus 103.36 red fox detections/100 trap nights in 2016), and by 2018, red fox trap success had decreased by almost 90% compared to that of 2016 (8.30 red fox detections/100 trap nights in 2018, Figure 32).

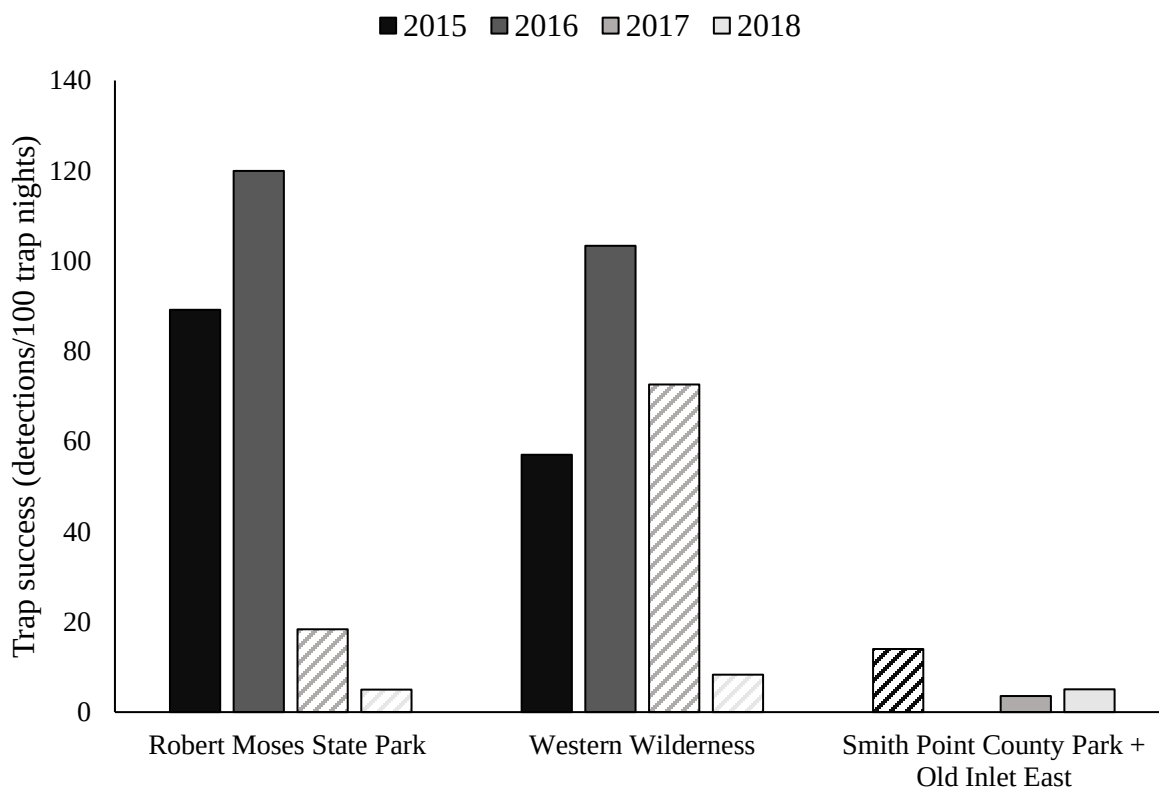


Figure 32. Observed red fox trap success (detections/100 trap nights) by site during each remote camera survey period on Fire Island, New York in 2015–2019. Remote camera surveys were conducted in September–February of each year, ending in February 2019. Solid bars indicate survey periods before or after mange outbreaks at each site, and hashed bars indicate survey periods during mange outbreaks. No red foxes were detected at Smith Point County Park + Old Inlet East during the 2016 camera surveys.

Top occupancy models differed across sites and years in whether detection probability was best modeled as constant or varying by day (Table 26). At Smith Point County Park and Old Inlet East,

occupancy remained stationary across all years that red foxes were present, ranging from 0.82-0.86, but dropped to 0 in the year following the mange outbreak (Table 27, Figure 33). Red foxes were detected at all stations in Robert Moses State Park and the Western Wilderness prior to the arrival of mange in those study sites in 2017, resulting in an occupancy estimate of 1 (Table 27, Figure 33). At Robert Moses State Park, occupancy declined relatively little during and after the mange outbreak (0.97 and 0.82 in 2017 and 2018, respectively), with 95% confidence intervals still reaching up to or approaching 1 (Table 27, Figure 33). This same pattern was observed in the Western Wilderness, where occupancy was 1 in 2015 and 2016, and in 2017 as the mange outbreak at this site was beginning. Occupancy decreased to 0.86 in 2018, when the outbreak was still ongoing, but 95% confidence intervals still included 1 (Table 27, Figure 33). Detection probabilities in all study sites varied, but generally decreased during and after the mange outbreaks (Table 27).

Table 26. Model selection tables for red fox occupancy (ψ) and detection probability (p) for each site and survey period on Fire Island, NY in 2015-2019. AIC = Akaike's Information Criterion.

Site	Model ^a	AIC	Δ AIC	Model weight	Model Likelihood	# of Parameters
Fall 2015–Winter 2016						
Robert Moses State Park	$\psi(.) p(\text{day})$	1953.57	0.00	1.0	1.0	53
	$\psi(.) p(.)$	2021.14	67.57	0.0	0.0	2
Western Wilderness	$\psi(.) p(\text{day})$	1985.15	0.00	1.0	1.0	62
	$\psi(.) p(.)$	2000.60	15.45	0.0	0.0	2
Smith Point County Park +	$\psi(.) p(\text{day})$	1098.50	0.00	1.0	1.0	47
Old Inlet East	$\psi(.) p(.)$	1124.24	25.74	0.0	0.0	2
Fall 2016–Winter 2017						
Robert Moses State Park	$\psi(.) p(.)$	2257.46	0.0	1.0	1.0	2
	$\psi(.) p(\text{day})$	2292.93	35.47	0.0	0.0	62
Western Wilderness	$\psi(.) p(.)$	2176.80	0.00	0.99	1.0	2

	$\psi(.)$ $p(\text{day})$	1886.26	9.46	<0.01	<0.01	58
Smith Point County Park +	N/A					
Old Inlet East	N/A					
Fall 2017–Winter 2018						
Robert Moses State Park	$\psi(.)$ $p(\text{day})$	1552.64	0.00	0.99	1.0	67
	$\psi(.)$ $p(.)$	1569.44	16.80	<0.01	<0.01	2
Western Wilderness	$\psi(.)$ $p(.)$	2062.46	0.00	0.99	1.0	2
	$\psi(.)$ $p(\text{day})$	2072.23	9.77	<0.01	0.0	59
Smith Point County Park +	$\psi(.)$ $p(\text{day})$	413.14	0.00	1	1	2
Old Inlet East	$\psi(.)$ $p(.)^b$					
Fall 2018–Winter 2019						
Robert Moses State Park	$\psi(.)$ $p(\text{day})$	663.16	0.00	1.0	1.0	58
	$\psi(.)$ $p(.)^b$					
Western Wilderness	$\psi(.)$ $p(\text{day})^b$	966.77	0.00	0.72	1.0	80
	$\psi(.)$ $p(.)$	968.63	1.86	0.28	0.4	2
Smith Point County Park +	$\psi(.)$ $p(.)$	684.08	0.00	1.0	1.0	2
Old Inlet East	$\psi(.)$ $p(\text{day})$	722.67	38.59	0.0	0.0	54

^a (.)= constant, N/A=unable to model due to lack of detections

^b Model did not converge

Table 27. Occupancy (ψ) and detection probability (p) estimates from top models of red fox occupancy for each site and survey period on Fire Island, New York in 2015–2019. If detection probability was best modeled as a constant value, that value and the standard error (in parentheses) are shown. If detection probability was best modeled as varying by day, the range of estimated daily detection probabilities is shown.

Site	Fall 2015– Winter 2016		Fall 2016– Winter 2017		Fall 2017– Winter 2018		Fall 2018– Winter 2019	
	Ψ	p	Ψ	p	Ψ	p	Ψ	p
Robert Moses State Park	1	0.03-0.72	1	0.67 (0.01)	0.97 (0.03) ^b	0.03-0.38 ^b	0.82 (0.07) ^b	0.00-0.18 ^b
Western Wilderness	1	0.11-0.61	1	0.54 (0.01)	1 ^a	0.42 (0.01) ^a	0.86 (0.07) ^b	0.08 (0.01) ^b
Smith Point County Park + Old Inlet East	0.86 (0.06) ^b	0.03-0.25 ^b	N/A ^{c,d}	N/A ^{c,d}	0.84 (0.12) ^c	0.04-0.14 ^c	0.80 (0.08) ^c	0.06 (0.01) ^c

^a Mange first detected at the site

^b During mange outbreak at that site

^c After mange outbreak at that site

^d N/A=unable to model due to lack of detections

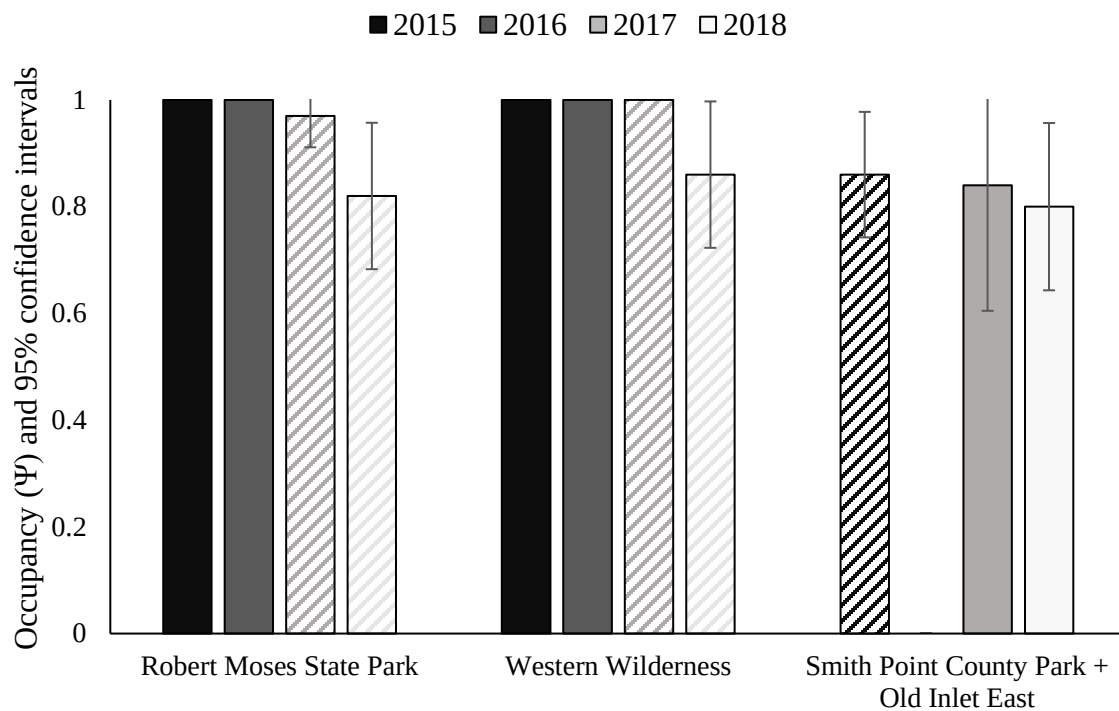


Figure 33. Red fox occupancy estimates $\pm$ 95% confidence intervals by site during each remote camera survey period on Fire Island, New York from 2015–2019. Remote camera surveys were conducted in September–February of each year, ending in February 2019. Solid bars indicate survey periods before or after mange outbreaks at each site, and hashed bars indicate survey periods during mange outbreaks. No red foxes were detected at Smith Point County Park + Old Inlet East during the 2016 camera surveys.

Reproduction

We observed pronounced decreases in reproduction in the breeding seasons following the detection of mange at each site (Table 28). At Robert Moses State Park and the Fire Island National Seashore Lighthouse Tract, the number of breeding groups in 2017 ($n = 4$), as the mange outbreak at that site was beginning, was identical to that of 2016 (pre-mange). Although the number of breeding pairs stayed constant between 2016 and 2017, average litter size decreased by 20% compared to the 2016 average ($\bar{x} = 3.5$ (0.5 SE) kits/den in 2016 to $\bar{x} = 2.8$ (0.5 SE) kits/den in 2017). In 2018, there was a complete reproductive failure at Robert Moses State Park and the Lighthouse Tract, with no breeding groups or breeding dens observed. In the Western Wilderness, where mange was not

detected until after the 2017 breeding and kit-rearing seasons, there were fewer than half as many breeding groups and a 72% decrease litter size from 2016 to 2017 ($n = 5$ breeding groups with $\bar{x} = 3.6$ (0.9 SE) kits/den in 2016 and $n = 2$ breeding groups with $\bar{x} = 1$ (0 SE) kits/den in 2017). Again, there was a complete reproductive failure at this site in 2018, while the mange outbreak was underway. At Smith Point County Park and Old Inlet East, there was a complete reproductive failure in 2016-2018 with no active breeding dens, kits, or other signs of successful reproduction found at that site through the end of data collection. Litter sizes were similar before versus during mange outbreaks across sites (Kruskal-Wallis test, $\chi^2_1 = 0.04$, $P = 0.84$). We did not compare litter sizes before versus after outbreaks, given the complete reproductive failure after mange outbreaks at each site during our study period.

Survival/mortality

The proportion of GPS-collared red foxes surviving to the end of the GPS-tracking period varied among sites and years, ranging from 75-100% at each site prior to the arrival of mange and decreasing to 0-38% by site during and following the outbreaks (Table 29). The proportion of GPS-collared red foxes across sites that survived to the end of the GPS-tracking period was significantly lower during mange outbreaks than before outbreaks ($\chi^2_1 = 15.02$, $P \leq 0.001$). We did not have any GPS-collared red foxes east of Old Inlet after the first outbreak, and the outbreak west of Old Inlet was ongoing at the end of data collection. Thus, we did not compare survival before versus after outbreaks.

Table 28. Number of red fox breeding groups monitored and mean (SE) number of kits per breeding group by site, and the months in which sarcoptic mange was first detected in red foxes each site, on Fire Island, New York in April–August of 2016–2018. These counts include all kits that survived through the end of the kit-rearing period, using August 1 as a cutoff.

Site	Mange first detected	2016		2017		2018	
		Breeding groups	Mean kits/group (SE)	Breeding groups	Mean kits/group (SE)	Breeding dens	Average kits/group (SE)
Robert Moses State Park + Lighthouse Tract	May 2017	4	3.5 (0.5)	4 ^a	2.8 ^a (0.5)	0 ^b	N/A
Western Wilderness	October 2017	4	3.6 (0.9)	2	1 (0)	0 ^b	N/A
Smith Point County Park + Old Inlet East	September 2015	0 ^c	0 ^c	0 ^c	0 ^c	0 ^c	N/A
All sites		8	3.5 (0.6)	6	2.2 (0.5)	0	N/A

^aMange first detected at the site

^bDuring mange outbreak at that site

^cAfter mange outbreak at that site

Table 29. Number of GPS-collared red foxes (N) and the proportion of those foxes known to have survived to the end of each GPS collar tracking period on Fire Island, New York in 2015–2018. GPS collar tracking periods spanned August 2015–March 2016, April–August 2016, and February–August 2017 and 2018.

Site	Mange first detected	2015		2016		2017		2018	
		N	Proportion survived	N	Proportion survived	N	Proportion survived	N	Proportion survived
Robert Moses State Park + Lighthouse Tract	May 2017	5	1.00	6	1.00	8	0.38 ^a	3 ^b	0.33 ^a
Western Wilderness	October 2017	2	1.00	5	1.00	4	0.75	0	N/A ^a
Smith Point County Park + Old Inlet East	September 2015	3	0.00 ^a	0	N/A	0	N/A	0	N/A
All sites		10	0.64	11	1.00	12	0.50	3	0.33

^aDuring mange outbreak at that site

^bOne fox's GPS collar was dropped early due to malfunction; we were able to identify this fox by their ear tag and verify survival through the end of the collar tracking period based on remote camera photos taken at non-breeding dens

Of 14 GPS-collared and/or ear-tagged adult red foxes that were found dead during the study, complications of mange were the most common suspected cause of death (n=8), followed by vehicle collisions (n=2), unknown causes (n=2), poaching (n=1) and drowning (n=1). In addition to these adult mortalities, two red fox kits were found dead during the 2017 kit-rearing period; one was found dead of unknown causes during a den monitoring visit, and the other was found by project collaborators dead of a suspected vehicle collision along an ORV road. Four red foxes were removed from the study area by humans (taken to a local wildlife rehabilitator for treatment of mange/injuries, n=3; removed by U.S. Department of Agriculture's Animal and Plant Health Inspection Service (USDA-

APHIS) Wildlife Services, n=1) during the data collection period, and were not included in our analyses.

Minimum red fox abundance and density estimates

At Smith Point County Park and Old Inlet East, red fox abundance and density were lowest in February–August 2016, following the outbreak at that site over the prior year (2016: 0 red foxes, 0 foxes/km², 5.94 km² total site area, Table 30, Figure 34), and remained relatively low throughout the rest of our study (2017 and 2018: 1 red fox, 0.17 foxes/km²). At Robert Moses State Park and the Fire Island National Seashore Lighthouse Tract, abundance and density were highest in February–August 2017, with the first detected signs of mange observed roughly halfway through this census period (2017: 29 red foxes, 6.26 foxes/km², 4.63 km² total site area), and had decreased substantially by the 2018 census period (2018: 5 red foxes, 1.08 foxes/km²). In the Western Wilderness, abundance and density were highest in February–August 2016, before the arrival of mange (2016: 35 red foxes, 9.09 foxes/km², 3.85 km² total site area), but decreased substantially afterwards (2018: 1 red fox, 0.26 foxes/km²). Minimum red fox density differed before, during, and after mange outbreaks across sites (Kruskal-Wallis test, $\chi^2_2 = 6.01$, $P \leq 0.05$), with higher densities observed before versus after outbreaks (post-hoc Dunn test, $Z = -2.39$, $P < 0.01$).

We collected and sent 268 potential red fox scat samples to the MECU for genetic analyses. 71 samples contained sufficient DNA to yield an individual red fox identification via microsatellite genotyping, resulting in the detection of 48 unique genotypes across samples collected from April 2016–February 2019. Four of the 7 tissue samples from dead red foxes contained sufficient DNA for individual identification, yielding 3 additional unique genotypes for a total of 51 different genotypes detected during the study. We identified fewer unique genotypes per year in years following the mange outbreaks, with 32 genotypes identified in 2016 samples (prior to the outbreak west of Old Inlet, n= 130 scats and 4 tissue samples) and 12 and 14 genotypes identified in samples from 2017 (n= 100 scats and 2 tissue samples) and 2018–February 2019 (n= 38 scats and 1 tissue sample),

respectively. Of the 32 unique genotypes sampled from scats or tissue collected in 2016, 5 genotypes (15.6%) were detected again in 2017. Of the 12 unique genotypes sampled in 2017, 2 genotypes (16.7%) were sampled in 2018. Only one genotype that was sampled in 2016 was sampled again in 2018. Overall, only 13.7% of unique genotypes were sampled in multiple years.

Table 30. Information used to calculate minimum red fox abundances and densities at each study site from February–August of 2016–2018 on Fire Island, New York. We estimated minimum red fox abundance by adding together: the number of GPS-collared adults monitored, the number of additional adults ear-tagged, the number of adults associated with each breeding group monitored (if those adults were not included in counts of collared and ear-tagged foxes); the number of kits associated with each breeding group; and any other known individuals observed during the census period (1 February–1 August). We then estimated minimum red fox density by dividing the minimum red fox abundance by the area of each site (4.63 km² for Robert Moses State Park + Lighthouse Tract, 3.85 km² for the Western Wilderness, and 5.94 km² for Smith Point County Park + Old Inlet East).

Site	Year	GPS-collared adults	Ear-tagged adults	Adults at dens	Kits	Other known individuals	Minimum abundance	Minimum density (foxes/km ²)
Robert Moses	2016	6	0	5	14	0	25	5.40
State Park +	2017	8	2	5	13	1	29 ^a	6.26
Lighthouse Tract	2018	2	1	1	0	1	5 ^b	1.08
Western	2016	5	1	11	18	0	35	9.09
Wilderness	2017	4	3	4	2	0	13 ^c	3.38
	2018	0	0	0	0	1	1	0.26
Smith Point	2016	0	0	0	0	0	0	0.00
County Park +	2017	0	0	0	0	1	1	0.17
Old Inlet East	2018	0	0	0	0	1	1	0.17

^a5 adults and 2 kits included in this count died during the census period

^b2 adults included in this count died during the census period

^c1 adult included in this count died during the census period

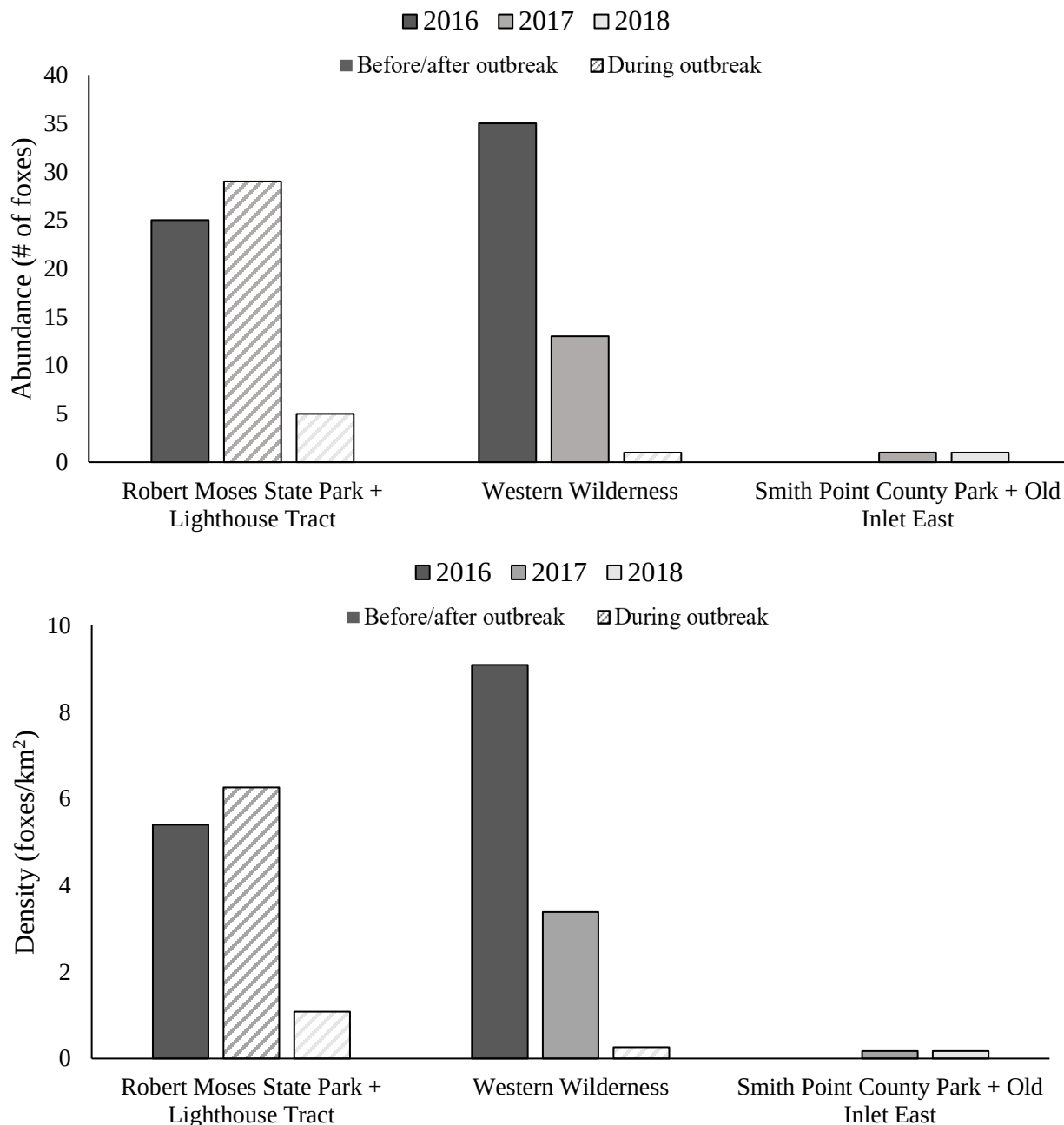


Figure 34. Minimum estimated red fox abundance (top) and density (bottom) by site in February–August of 2016–2018 on Fire Island, New York. Solid bars indicate census periods before or after mange outbreaks at each site, and hashed bars indicate census periods during mange outbreaks. No red foxes were detected at Smith Point County Park + Old Inlet East during the 2016 census period.

We observed one red fox with moderate signs of mange and several sets of fox tracks during our October 2018 driving surveys through the Fire Island villages but did not encounter any reliable red fox signs during subsequent surveys in November 2018–February 2019. We received 6 reports of red fox sightings in the villages from NPS staff ranging from August–December 2018 (Table 31), 3 of which included photographs verifying the animals’ conditions. Red foxes in the 4 sightings reported prior to 11 December 2018 did not appear to be affected by mange, while those in the 2 sightings after that date showed signs of mild to moderate mange.

Table 31. Summary of red fox sighting reports received from National Park Service staff on Fire Island, New York from August 2018–February 2019. All reports described one observation of a single fox, unless otherwise noted.

Month/Date	Location	Signs of mange?	Photos?
August 2018	Sailor’s Haven	No	No
September 2018 ^a	Watch Hill	No	No
10/17/2018	Wilderness Area (West of Old Inlet)	No	Yes
12/4/2018	Robin’s Rest	No	No
12/11/2018	Kismet	Yes, moderate	Yes
12/12/2018	Sailor’s Haven	Yes, mild-moderate	Yes

^a One report of multiple sightings (number unspecified) of a fox at this location during September 2018.

Discussion

Our combined observations from monitoring GPS-collared and ear-tagged foxes, transect surveys, den monitoring, remote camera surveys, and genetic analyses of scat provide multiple lines of evidence indicating a dramatic decline in red fox trap success, relative abundance, minimum density, annual reproduction, and survival following the mange outbreaks at each site.

The observed proportion of fox deaths attributable to mange (57% of all known deaths) and population declines (complete die-off east of Old Inlet following the first outbreak, 83% and 97% decreases in minimum abundance and density estimates at sites west of Old Inlet following the second outbreak) are on par with the dramatic mortality rates and declines reported in some previous studies of mange outbreaks in fox populations (Mörner 1992, Baker et al. 2000, Soulsbury et al. 2007).

Despite these observed decreases in relative abundance and density, reproduction, and survival, we observed high occupancy in all years and sites where foxes were present. With the exception of the ~1-year period where red foxes apparently were absent east of Old Inlet and in Smith Point County Park, our occupancy estimates across all sites and years were all ≥ 0.80 , with confidence intervals up to or approaching 1. This was true even for survey periods during which we believe that very few foxes were present. For example, we suspect that there may have been only one fox using Smith Point County Park and Old Inlet East in 2017 and 2018. During our transect surveys in 2017 and 2018, we observed no fox sign at Smith Point County Park and Old Inlet East for weeks or months at a time, and relatively little fox sign at other times. These results suggest that the remaining foxes during and after mange outbreaks likely expanded their use areas into former territories of dead foxes, leading to a lower overall population size but no significant decrease in occupancy based on overlapping 95% confidence intervals. For example, the last 3 remaining GPS-collared red foxes east of Old Inlet in 2015 all exhibited transient behavior, and moved regularly between Old Inlet and the middle of Smith Point County Park (1 female) or all the way to Moriches Inlet at the eastern end of the island (2 males, *Chapter 2*). Further, mange was a significant predictor of the size of a red fox's core use area, with foxes with mange using larger areas than foxes without mange (*Chapter 2*). This wide-

ranging behavior among remaining animals has been reported in other studies where a territorial species experienced a sharp population decline, including a long-term study of an urban fox population affected by mange in Bristol, UK (Baker et al. 2000, Potts et al. 2013).

Previous studies have reported much lower estimates of red fox occupancy in coastal systems. Gieder (2015) reported occupancy estimates ≤ 0.5 across all years and sites in their study on Assateague Island, MD and an average occupancy estimate of $0.43(\pm 0.04 \text{ SE})$. O'Connell et al. (2006) also reported lower red fox occupancy estimates on Cape Cod, MA ($0.35 \pm 0.17 \text{ SE}$). We acknowledge that the observed deaths of several foxes due to mange during some of the remote camera survey periods violated the closure assumption of occupancy modeling, meaning that detection probabilities later in those surveys could have been underestimated (Mackenzie et al. 2006). Thus, the occupancy estimates presented here are more accurately described as occurrence, rather than true occupancy.

When the observed mange die-offs are considered as a potential proxy for intensive lethal removal of foxes, our results suggest that even if removal activities could result in decreased fox abundance and density, they may not be effective in reducing the overall distribution of foxes unless complete eradication can be achieved. Previous studies have found that lethal removal of red foxes may not be effective at reducing occupancy in many cases. Although red fox occupancy on Assateague Island was lower throughout Gieder's (2015) study, it did not decrease despite annual red fox removal efforts. However, these removal efforts had been ongoing since 2009, before that study began, thus, Gieder's (2015) results may not have captured any initial response to removal activities. In some cases, lethal removal may actually have the opposite effect, leading to increased occupancy via colonization of previously unoccupied sites and/or compensatory reproduction. For example, Towerton et al. (2011) found that foxes colonized previously unused sites following lethal removal. In addition, previous studies of red fox population responses to lethal removal call into question whether removal efforts would succeed in reducing the overall population size, regardless of occupancy levels, due to compensatory immigration (Greentree et al. 2000, Baker and Harris 2006, Harding et al. 2001).

Increased reproduction among remaining individuals also has been identified as a potential factor counteracting lethal removal efforts. For example, Marlow et al. (2016) observed significantly larger litter sizes following artificial decreases of ~26% in fox density compared to litter sizes at a control site. We did not observe such increases after the mange-related population declines in our study area during the time period of our study (i.e., 0-2 years of post-mange data). Instead, we observed complete reproductive failure in breeding seasons following mange outbreaks at each site, likely related to the low number and poor condition of any remaining foxes. We also observed fewer breeding groups and fewer kits per litter in the Western Wilderness in 2017, prior to the arrival of mange at the site, suggesting that factors other than mange likely influenced reproduction on the island as well. Mange has previously been shown to reduce the proportion of individual foxes breeding within a population. In their study of the impacts of mange on a population of foxes in Bristol, UK, Soulsbury et al. (2007) found no evidence of breeding among severely affected females, and severely affected males apparently failed to produce sperm during the breeding period. Interestingly, mange may not affect the reproductive success of animals that are still able to reproduce during and after outbreaks, as Soulsbury et al. (2007) found that average litter sizes remained comparable among pre-mange, epizootic, and enzootic periods.

Management Implications

We found that red fox occupancy may remain high even after substantial decreases in abundance and population density following mange outbreaks. When considered as a proxy for intensive lethal removal, these results highlight the idea that, while such removal efforts may reduce predator abundance and population density within a given area, they may not be effective in reducing the overall distribution of red foxes or eliminating the risk of predation by red foxes in a given area.

Section 2: Red Fox Spatial Ecology

This section describes data collection, analytical methods, and results related to the following objectives for red fox monitoring associated with the Fire Island Inlet to Moriches Inlet Fire Island Stabilization Project during the 2015-2020 monitoring period. We were not able to collect additional field data in 2020 due to covid-19 restrictions.

Objective 2: Assess habitat use versus availability by red foxes and any variation in habitat selection related to changing habitat composition and predator management.

Objective 3: Quantify home range size, long-range movements, and variation in movement ecology of red foxes and relate to changing habitat composition and predator management.

Introduction

The red fox (*Vulpes vulpes*) has the largest geographic distribution of all terrestrial carnivores, and inhabits a wide variety of ecosystems (Lloyd 1980, Macdonald 1987, Macdonald and Sillero-Zubiri 2004). Like many canids, red foxes are highly adaptable in their ecology, and may alter their behavior in response to changing conditions (Goszczyński 2002). Red foxes have been extensively studied, leading to a large body of information about the species. Many of these studies have focused on red fox spatial ecology and habitat use, spanning a wide range of geographic locations and ecosystems (see Lloyd 1980, Ables 1983, Cavallini 1996, Goszczyński 2002, Baker and Harris 2004 *and others for reviews*). However, there are relatively few published studies of red fox spatial ecology in coastal ecosystems, particularly in North America.

The red fox is a key predator of the federally threatened piping plover (*Charadrius melodus*) along the North American Atlantic coast, leading to frequent red fox management aimed at reducing predation on these and other shorebirds (Hunt et al. 2019a). Information on red fox home range size, activity patterns, and habitat selection in coastal ecosystems can be used to predict relative predation risk over space and time and inform decisions about the spatial scale of management activities. Information on red fox ecology in barrier island ecosystems is particularly needed, as several previous

studies of piping plovers in these settings have identified red fox predation as an issue (Rimmer and Deblinger 1990, Patterson et al. 1991, Cohen et al. 2010, U.S. Fish and Wildlife Service 2014, Gieder 2015).

Previous studies of red fox spatial ecology on barrier islands are limited in number and geographic range. On Assateague Island, Virginia, Krim et al. (1990) examined den site selection relative to available habitat, Brittinger (1993) described home range sizes and dispersal of juvenile red foxes, and Gieder (2015) examined red fox occupancy patterns and movements using remote cameras. In southern New Jersey, Stantial et al. (2020) examined red fox occupancy relative to landscape features using track surveys. However, to our knowledge, there are no previous studies that have tracked individual adult red foxes on barrier islands, and thus no published information on adult home range sizes, diel activity patterns, or within-home range habitat selection of red foxes in these settings. As such, it is unknown how the unique geomorphic characteristics of barrier islands may impact these components of red fox spatial ecology, and to what extent managers can use information from studies conducted in other settings to infer relative risk of predation by red foxes across the island landscape. Barrier islands are relatively long and narrow compared to other geomorphic landforms used by red foxes, with generally linear distribution of habitat types that runs parallel to the length of the island. These factors could affect home range shapes and sizes and habitat selection patterns in response to varying resource distribution. In addition, the surrounding ocean areas may present a barrier to immigration, emigration, and juvenile dispersal, which could in turn influence the proportion of resident vs. transient animals within the population.

Our objectives were to estimate home range and core use area sizes, describe daily activity patterns, and investigate habitat selection among red foxes on Fire Island, New York, and to identify factors influencing each of these aspects of red fox ecology on the island. We also sought to evaluate the effect of sarcoptic mange on these aspects of red fox ecology, in response to a series of mange outbreaks that occurred on the island during this study (*Part 3, Section 1*), Robertson et al. 2019). We used these results to predict relative habitat suitability for red foxes within the study area, including in

two restoration areas intended to create piping plover habitat, to provide an index of relative predation risk that could be used to guide management.

Methods

Red fox trapping, GPS collaring, and tracking

We used Victor 1 ½ Soft Catch and Bridger #2 padded foothold traps to capture foxes in each monitoring area in August–November 2015, April–May 2016, and February–April 2017 and 2018, following the Association of Fish and Wildlife Agencies’ Best Management Practices for Trapping Red Foxes in the United States (AFWA 2014). Traps were set to require at least 2 lbs. of pressure to avoid capturing lighter animals and minimize the chance of capturing non-target species. Upon capture, we manually restrained foxes, determined their sex and breeding status, and collected morphometric measurements. When allowed by area managers, we also placed a colored plastic numeric ear-tag (Premier 1 Supplies, Washington, IA) or small metal ear-tag (National Band and Tag Company, Newport, KY) in the right ear, to aid in identifying individuals that were observed in the field and/or recaptured during subsequent trapping periods.

We outfitted up to 6 foxes per year in each management unit (i.e., the county, state, and national parks) with GPS collars (Quantum 4000E, medium size; Telemetry Solutions, Concord, CA) to collect location data. In 2015, we programmed collars to record GPS locations once per hour, every day for 30 days from their deployment date, and then once every two hours, on every other day, from day 31 through programmed collar drop-off (end dates varied depending on deployment date). In 2016–2018, we programmed collars to record GPS locations once every 1–2 hours, every day from April 20th through the end of May, then once every 2 hours, on every other day until programmed collar drop-off in early August. This variation in sampling schedule allowed us to extend collar battery life through the entire piping plover breeding season in 2016–2018 to meet data collection needs for additional project objectives. Every 10–14 days after deployment, we located collared foxes via radio telemetry tracking of the collar’s VHF signal and approached to within 10–200m to connect wirelessly

to the collar and download data using a UHF antenna, Quantum Base Station, and Collar SW v 2.09 software (Telemetry Solutions, Concord, CA). All field methods were approved by Virginia Tech's Institutional Animal Care and Use Committee (Protocol 15-119).

Covariates used in home range, activity, and habitat selection analyses

Variables used in our analyses of factors influencing red fox spatial ecology included season tracked (fall/winter or spring/summer), breeding status (associated with an active breeding den or not), and mange status (infected or not). Breeding status was determined by investigation of GPS location hotspots to search for active dens in the area. We also conducted concurrent den monitoring (*Part 3, Section 1*, Robertson et al. 2019) during the 2016–2018 GPS-tracking periods, which allowed us to confirm individual association with dens via in-person observations and/or detections on remote cameras set up at dens. Mange status was a binary variable reflecting whether or not an individual was affected by sarcoptic mange during the monitoring period, based on regular observations of each fox's condition during trapping, data downloads, opportunistic sightings, and collar and carcass recovery (for animals that died prior to the end of the planned monitoring period).

Prior to modeling, we tested for independence among covariates using Fisher's exact test (Fisher 1925, McDonald 2014). We tested all possible combinations of these categorical covariates. When variables were found to be correlated, we used Akaike's Information Criterion corrected for small sample size (AIC_c) to evaluate and compare univariate models, and retained whichever covariate better explained the data being considered as evidenced by the lower AIC_c . We included a unique identifier for each animal (animal ID) as a random effect in all models, to account for individual variation and multiple years of data from certain individuals. Once we had run all of our candidate models, we used Akaike's Information Criterion corrected for small sample size (AIC_c) to evaluate and compare models, considering those within 4 ΔAIC_c of the top-ranked model as competitive (Burnham and Anderson 2007).

Home range estimation and modeling

We only used locations that were designated as a “3D” fix in the collar output data, indicating sufficient satellite connection to reliability to estimate the latitude, longitude, and approximate altitude of a given location (Telemetry Solutions 2011). We excluded locations >10m into the ocean surrounding the island, or with recorded elevation values well above the highest known point on the island, assuming they were erroneous. We then used the ‘tlocoh’ package in R (Version 3.5.2, www.r-project.org, accessed 15 May 2019) to estimate 50% and 95% utilization distribution isopleths using a time local convex hull (T-LoCoH) approach with the k-LoCoH parameterization (Lyons et al. 2013). Like the original local convex hull (LoCoH) method, T-LoCoH is a nonparametric approach that is well-suited to situations in which hard geographic boundaries constrain animal movements (Getz et al. 2007, Lyons et al. 2013), as is often the case in barrier island ecosystems where the surrounding water acts as a movement barrier for terrestrial animals. T-LoCoH improves upon previous LoCoH methods by incorporating time into the nearest neighbor selection and hull construction processes (Lyons et al. 2013). We followed Lyons’ (2014) guidelines for interactive selection of scaling parameter s and number of nearest neighbors k at the individual level. We used the resulting 50% utilization distribution isopleths to represent each animal’s core use area, and the resulting 95% utilization distribution isopleths to represent each animal’s home range area.

Red foxes have been previously shown in the literature to exhibit both resident and transient space use (Cavallini 1996), with residents maintaining relatively small, consistent home ranges and transients using relatively large, shifting home ranges. The 50% and 95% utilization distribution isopleths of transient individuals within a population are more appropriately described as biding areas and transient ranges, respectively, than core use and home range areas (Hinton et al. 2015, Morin and Kelly 2017). We based our classification of residents and transients on factors that reflect the differences in both home range size and consistency in space use that we would expect between resident and transient foxes. We conducted a cluster analysis to sort red foxes into transient or resident status based on the following information: estimated home range size, maximum observed

distance to home range centroid across all locations, mean distance to home range centroid across all locations, standard deviation of observed distances to home range centroid, and the coefficient of variation (standard deviation/mean) of observed distances to home range centroid. Prior to running the cluster analyses, we calculated Pearson's correlation coefficient for each possible combination of these variables, and dropped metrics that were strongly correlated with other metrics (Pearson's correlation coefficient >0.70) from our analyses. We then used the "vegdist" function in R package 'vegan' (Version 2.5-6, <https://github.com/vegandevs/vegan>, Accessed 2 July 2020) and "hclust" function in R package 'stats' (Version 3.6.2, <https://www.rdocumentation.org/packages/stats/versions/3.6.2>, Accessed 2 July 2020) to run the cluster analysis, and the "as.dendrogram" function in R package 'stats' (Version 3.6.2, <https://www.rdocumentation.org/packages/stats/versions/3.6.2>, Accessed 2 July 2020) to visualize the resulting groupings of transient and resident foxes based on these variables.

Following home range and core use area estimation and resident vs. transient classification, we used generalized linear mixed modeling (GLMM) to examine the impacts of covariates (season, sex, breeding status, mange status) on home range and core use area sizes of both resident and transient foxes.

Activity patterns and modeling

We estimated hourly movement rates to serve as an index of red fox activity patterns, dividing the straight-line distance between successive locations by the time difference between those locations to calculate movement rates in meters/hour (Rockhill et al. 2013). We excluded movements between locations with a time difference <0.8 hours or >4 hours from these analyses, to mitigate potential bias due to duplicated locations or missed GPS fixes. The resulting movement rates were used to calculate an average movement rate for each individual for each hour of the day, corrected for seasonal differences in sunrise time.

We used generalized linear mixed modeling (GLMM) to compare the impacts of covariates (season, sex, breeding status, range status) on individual average hourly movement rates. We also included the animals' residency status (resident or transient), and the number of hours since sunrise (to test for differing activity levels throughout the day) in these analyses. To account for potential variation in habitat selection during active vs. resting periods in later analyses, we attempted to group hours with similar mean movement rates, based on overlapping 95% confidence intervals, into diel activity period categories.

Within-home range habitat selection

To investigate within home range habitat selection (3rd order selection, Johnson 1980), we compared used vs. available locations using a series of distance-based resource selection function analyses (Conner et al. 2001, Manly et al. 2002). Distance-based resource selection approaches are more robust to location uncertainty than classification-based approaches, and allow for investigation of selection patterns that are more difficult to address using classification-based approaches, such as edge effects and selection for linear and point features (Conner et al. 2003). Because many red foxes are territorial, not all areas are equally available to all individuals. Thus, we randomly simulated 5 locations per used location within a given animal's 100% minimum convex polygon (MCP), clipped to the extent of the island, to approximate availability at the individual level (Cooper and Millsaugh 1999, 2001).

We used 15-cm resolution landcover classification layers created using annual aerial imagery to characterize habitat across the island (Bellman 2018; Robertson et al. 2019). To minimize classification errors due to overlapping spectral signatures of anthropogenic and natural features, areas of human development (i.e. paved roads, parking lots, buildings, and residential areas) were delineated by hand and separated from the imagery prior to classification. The 'Maximum Likelihood Classification' tool in ArcGIS was then used to classify pixels into one of 5 habitat types: water, wet sand, dry sand, evergreen vegetation (primarily pitch pine *Pinus rigida* woodland and maritime forest), and all other

vegetation (primarily beachgrass, other herbaceous vegetation, and deciduous shrubs). We created additional shapefiles in ArcGIS delineating off-road vehicle (ORV) roads. These routes are unpaved, primarily on dry sand, and are regularly used for access to recreation and residential areas. We hypothesized that they could serve as travel corridors for foxes and other wildlife. Conversely, they also could be areas with increased risk of human encounters and vehicle-fox collisions. We resampled the original 15-cm resolution layers to create 1-m resolution layers for our analyses, assigning each 1-m cell to the majority habitat type of the 15-cm cells that it contained. We used these coarser classification layers and the “Euclidean Distance” tool in ArcMap to create 1-m resolution distance-to rasters for each habitat type and ORV roads. We then overlaid all used and random locations onto these distance rasters and extracted the estimated distances, and appended attribute data for individual foxes to create input data for resource selection function analyses.

Prior to modeling, we tested for independence among covariates using Fisher’s exact test and z-standardized continuous covariates (Fisher 1925, McDonald 2014). We then used the “glmer” function in R package ‘lme4’ (Version 1.1-21, <https://github.com/lme4/lme4>, Accessed 14 November 2019) to run several mixed effects logistic regression models, with whether a location was used or random as the response. We compared a model that included the distances to all 7 habitat types and features of interest (development, water, wet sand, dry sand, evergreen vegetation, all other vegetation, and ORV roads) to a set of additional models, which included the distances to these 7 habitat types plus one of the attribute covariates of interest (season, sex, breeding status, mange status, residency, and diel activity period) as either an additive or interactive effect. Interactive effects were included in models as interacting with all 7 habitat types. We used Akaike’s Information Criterion corrected for small sample size (AIC_c) to evaluate and compare models (Burnham and Anderson 2007), and used k-fold cross-validation to assess the predictive power of the top supported model (Boyce et al. 2002).

Landscape-scale habitat selection of red foxes

We also used distance-based resource selection function analyses to investigate landscape-scale (2nd order, Johnson 1980) habitat selection of red foxes (Conner et al. 2001, Manly et al. 2002). While the habitat selection analyses described above were focused on how foxes selected habitat within their home range (Johnson's 3rd order), these landscape-scale analyses investigated how foxes selected from the available areas, establishing that home range (Johnson 1980). By explicitly examining the factors influencing home range selection, we can use the resulting coefficients to infer the relative likelihood that a given part of the study area will be included in one or more fox's home range. To allow for potential future comparisons between landscape-scale habitat suitability for red foxes and piping plovers, we limited this set of analyses to locations collected during the piping plover breeding season.

We compared used to available locations to identify factors influencing probability of use. We randomly simulated 5 locations within the relevant fox trapping/monitoring area per used location to approximate availability. To account for the fact that our trapping efforts were not evenly distributed across the island, we limited both the used locations in our analyses and the areas from which random points were drawn to the areas that our trapping efforts covered in corresponding years (Figure 35).

As with our 3rd order resource selection function analyses, we used the "extract" function in the 'raster' R package (Version 2.9-23, <https://rspatial.org/raster/>, Accessed 14 November 2019) to extract and append distances from locations to each habitat type, and appended attribute data for individual foxes to create our input data for 2nd order resource selection function analyses. We randomly sorted 75% of our created resource selection function input data to create our models, leaving 25% as a testing dataset that we used to evaluate the predictive accuracy of our models. We then used the same modeling approach that we used for our within-home range habitat selection analyses to compare a series of models for landscape-scale habitat selection.

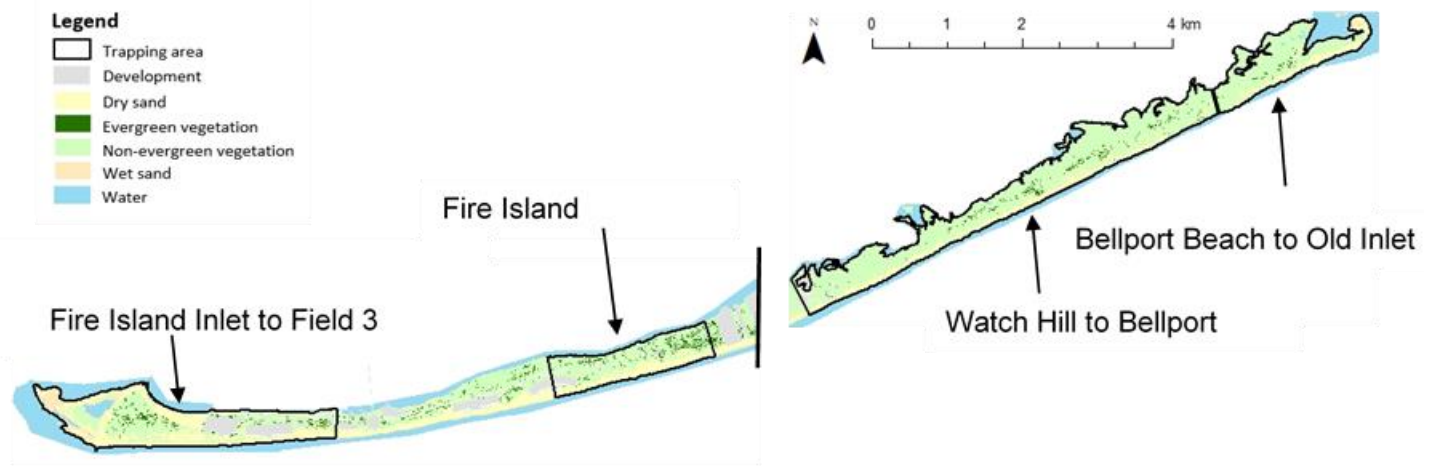


Figure 35. Boundaries that were used to guide red fox trapping efforts on Fire Island, New York in 2016 and 2017, overlaid onto 2017 landcover classification data. These boundaries were used to constrain locations used and available locations included in landscape- level (2nd order) habitat selection analyses. 2016 trapping efforts and analyses included the area from Fire Island Inlet to Field 3 at Robert Moses State Park and the area from Watch Hill to Old Inlet. 2017 trapping efforts and analyses included the area from Fire Island Inlet to Field 3 at Robert Moses State Park, the Fire Island Lighthouse Tract, and the area from Bellport Beach to Old Inlet.

Island-wide habitat suitability predictions for red foxes

We used the "Raster Calculator" tool in ArcMap 10.6 (ESRI 2018, Redlands, CA) to z-standardize each of our distance rasters using the same mean and standard deviation values that were used to z-standardize the corresponding habitat covariates, then projected the coefficients and equation from our top supported model from the landscape-scale (Johnson's 2nd order) analyses onto the study area, clipped to the extent of the island. The values in this layer do not reflect the true probability of use, rather they are a measure of relative suitability (Keating and Cherry 2004, Morris et al. 2016). We divided the resulting layer into both 5 and 10 equal area bins to allow for easier interpretation and accuracy assessment (Boyce et al, 2002, Morris et al. 2016). We used the 25% of the data that was not used to create the model to test the accuracy of our relative suitability prediction layers, comparing the predicted suitability in each binned area to the average relative suitability value of points falling in that bin. We repeated these steps using each year's landcover data and created separate maps for groups of foxes (i.e., males vs. females, residents vs. transients) that our modeling results suggested differed significantly in their habitat selection patterns. Finally, we overlaid these predictive habitat

suitability maps onto GIS layers delineating the boundaries of the 2 habitat restoration areas in our study area that were created by the U.S. Army Corps of Engineers to mitigate potential habitat loss related to post-Hurricane Sandy shoreline stabilization projects on the island, and used the “Zonal Statistics” tool in ArcMap to calculate mean predicted suitability values for each of these areas for each map created (USACE 2014, USFWS 2014).

Results

Red fox trapping, GPS collaring, and tracking

We captured and outfitted 36 red foxes with GPS collars and monitored them until programmed collar drop off, or until the fox died prior to collar drop off (Table 32). Two red foxes, individually-identifiable by ear tags, were recaptured, collared, and monitored over a second trapping period, resulting in two location datasets from those individuals and thus a total of 38 GPS monitoring datasets (Table 32). Collar malfunctions resulted in no usable data from 2 foxes, and insufficient data for analyses from 2 foxes. Another fox disappeared after collaring, and was never located again despite intensive searching across the island, yielding no usable data. Thus, we used 33 location datasets, collected from 31 individual collared foxes, for analyses.

Table 32. Identity, year and season monitored, site captured, resident versus transient categorization, reproductive status, mange infection status, and fate of GPS-collared foxes (n=36 unique foxes, 38 location datasets) on Fire Island, NY 2015-2018. F denotes females, M denotes males. Season abbreviations: F/W=Fall–Winter, SP/SU=Spring–Summer. Site abbreviations: RMFIL=Robert Moses State Park/Fire Island Lighthouse Tract, FINS=Fire Island National Seashore Wilderness Area (west of Old Inlet), SPOIE=Smith Point County Park/Fire Island National Seashore Wilderness Area (east of Old Inlet). Breeding and mange abbreviations: Y=Yes, N=No.

Fox	Year	Season	Site	Residency	Breeding	Mange	Fate
F-01	2015	F/W	RMFIL	Resident	N/A	N	Survived to end of monitoring period
M-01	2015	F/W	RMFIL	Transient	N/A	N	Survived to end of monitoring period
F-02	2015	F/W	RMFIL	Resident	N/A	N	Survived to end of monitoring period
M-02	2015	F/W	RMFIL	Transient	N/A	N	Survived to end of monitoring period
F-03 ^{a,b}	2015	F/W	RMFIL	Resident	N/A	N	Survived to end of monitoring period
M-03	2015	F/W	SPOIE	Transient	N/A	Y	Died December 2015, mange
M-04	2015	F/W	FINS	Transient	N/A	N	Survived to end of monitoring period
M-05	2015	F/W	FINS	-	-	-	Disappeared after GPS collaring, no usable data
M-06	2015	F/W	FINS	Resident	N/A	N	Survived to end of monitoring period
M-07	2015	F/W	SPOIE	Transient	N/A	N	Died January 2016, likely vehicle collision
F-04	2015	F/W	SPOIE	Transient	N/A	Y	Died March 2016, mange

M-08 ^b	2016	SP/SU	RMFIL	Resident	Y	N	Survived to end of monitoring period
F-05	2016	SP/SU	RMFIL	Resident	Y	N	Survived to end of monitoring period
M-09	2016	SP/SU	RMFIL	Resident	Y	N	Collar malfunction, insufficient data for analyses
M-10	2016	SP/SU	RMFIL	Transient	N	N	Survived to end of monitoring period
F-07	2016	SP/SU	RMFIL	Resident	Y	N	Survived to end of monitoring period
M-11	2016	SP/SU	RMFIL	Transient	N	N	Survived to end of monitoring period
M-12	2016	SP/SU	FINS	-	-	-	Collar malfunction, no usable data
M-13	2016	SP/SU	FINS	Resident	N	N	Survived to end of monitoring period
M-14	2016	SP/SU	FINS	Resident	N	N	Survived to end of monitoring period
F-08	2016	SP/SU	FINS	Resident	N	N	Survived to end of monitoring period
F-09	2016	SP/SU	FINS	Resident	N	N	Survived to end of monitoring period
F-10	2016	SP/SU	FINS	Resident	N	N	Survived to end of monitoring period
M-15	2017	SP/SU	RMFIL	Resident	N	N	Died August 2017, likely vehicle collision

F-11	2017	SP/SU	RMFIL	Resident	N	N	Survived to end of monitoring period
F-03 ^b	2017	SP/SU	RMFIL	Resident	N	N	Survived to end of monitoring period
F-12	2017	SP/SU	RMFIL	Resident	N	N	Survived to end of monitoring period
M-08 ^b	2017	SP/SU	RMFIL	Resident	Y	N	Died August 2017, likely drowned
M-16	2017	SP/SU	RMFIL	Transient	N	Y	Died June 2017, unclear whether from mange or drowning
M-17	2017	SP/SU	RMFIL	Resident	Y	Y	Died May 2017, mange
F-13	2017	SP/SU	RMFIL	Resident	Y	Y	Died August 2017, mange
F-14	2017	SP/SU	FINS	Resident	N	N	Survived to end of monitoring period
M-18	2017	SP/SU	FINS	Resident	N	N	Survived to end of monitoring period
F-15	2017	SP/SU	FINS	Resident	Y	N	Survived to end of monitoring period
F-16	2017	SP/SU	FINS	-	-	N	Died April 2017 of unknown causes, insufficient data for analyses
M-19 ^c	2018	SP/SU	RMFIL	Resident	N	Y	Died May 2018, likely mange
F-17 ^c	2018	SP/SU	RMFIL	Resident	N	N	Died May 2018, unknown cause

F-18	2018	SP/SU	RMFIL	-	-	Y	Collar malfunction, no usable data
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^a <300 locations recorded due to low GPS fix success rate

^b Recaptured and GPS-collared during multiple monitoring periods

^c <300 locations recorded due to death early in monitoring period

Sarcoptic Mange Outbreak

A sarcoptic mange outbreak began east of Old Inlet shortly after the start of our 2015 trapping efforts, with the first recorded signs of mange in a red fox in this study observed on 3 September 2015. This outbreak led to a substantial die-off of red foxes east of Old Inlet (*Part 3, Section 1*, Robertson et al. 2019). Following the death of the last GPS-collared red fox east of Old Inlet on 24 March 2016, red foxes were apparently absent in this area from April 2016–March 2017; we did not find any signs of red foxes during concurrent sign surveys and remote camera monitoring. We were unsuccessful in capturing or GPS-collaring any red foxes east of Old Inlet after March 2017.

A second sarcoptic mange outbreak began west of Old Inlet during the 2017 monitoring period, with the first recorded signs of mange in a red fox west of Old Inlet observed on 22 May 2017. Prior to this, no mange-like symptoms had been observed during the study in foxes west of Old Inlet. This outbreak also led to a substantial die-off of red foxes, this time west of Old Inlet (*Part 3, Section 1*, Robertson et al. 2019).

Home range estimation and modeling

GPS-collared red fox home range sizes (95% isopleths) varied widely, ranging from 10.09 ha - 658.55 ha ($\bar{x}$ = 164.44 ha, SE = 33.31 ha, n = 33; Figure 36). Core use (50% isopleths) area sizes also varied widely among individuals, ranging from 0.38 ha - 267.79 ha ($\bar{x}$ = 25.68 ha, SE = 8.51 ha, n = 33; Figure 36). Only home range size and the coefficient of variation of observed distances to home range centroids were included in cluster analyses, as these were the only two metrics that were not strongly correlated with the other metrics considered (correlation coefficients between all other metrics were

>0.75) nor with each other. Based on cluster analysis results, red foxes that maintained relatively small home ranges (10–165 ha) were classified as residents (n = 22), while red foxes that maintained relatively large home ranges (245–659 ha) were classified as transients (n = 9; Figure 37). The two groups had similar coefficients of variation of observed distances to home range centroids (residents: $\bar{x}$ = 0.84, SE = 0.08, n = 24; transients: $\bar{x}$ = 0.79, SE = 0.08, n = 9). Two transient males traveled the entire length of the island east of Old Inlet (~12 km) during the 2015 GPS tracking period, typically making the trip over ~1-3 days with regular multi-day stays in different localized areas in between. Two other transient males traveled the entire length of the island west of Old Inlet (~36 km) during their respective GPS-tracking periods (2015: n = 1, 2016: n = 1), typically making the trip over ~1 week with regular multi-day stays in different localized areas in between. We did not observe any red foxes crossing Old Inlet during the monitoring period, despite regular use of areas immediately adjacent to the inlet by multiple GPS-collared foxes (west of Old Inlet: n = 6, east of Old Inlet, n = 2). All males monitored in the fall/winter monitoring period (n = 6) exhibited transient behavior, but only 45% of males (n = 11) monitored in the spring/summer monitoring periods did so. Only one female, the last surviving GPS-collared fox east of Old Inlet following the first mange outbreak, exhibited transient behavior. We suspect that this red fox was the last surviving member of the red fox population east of Old Inlet, as we did not observe any red fox signs in the area for nearly a year after her death.

Season and sex most strongly influenced home range size, whereas season and mange status most strongly influenced core use area size (Table 33). Home ranges were smaller in the spring/summer monitoring periods ($\bar{x}$ = 115.30 ha, SE = 34.12 ha, n = 23; β = -0.50 $\pm$ 0.01 SE in top home range model) than in the fall/winter monitoring periods ($\bar{x}$ = 277.46 ha, SE = 38.15 ha, n = 10). Core use area were also smaller in the spring/summer monitoring periods ($\bar{x}$ = 20.17 ha, SE = 8.76 ha, n = 23; β = -0.33 $\pm$ 0.05 SE in top core use area model) than in the fall/winter monitoring periods ($\bar{x}$ = 38.35 ha, SE = 9.94 ha; n = 10). Male foxes used larger home ranges ($\bar{x}$ = 263.65 ha, SE = 34.12 ha, n = 17; male β = 0.62 $\pm$ 0.20 SE in top home range model) than females ($\bar{x}$ = 59.03 ha, SE = 34.34 ha, n =

16), but core use area size did not differ significantly between the sexes. Foxes affected by mange used similarly sized home ranges to healthy foxes, but foxes with mange used larger core use areas ($\bar{x}$ = 78.83 ha, SE = 12.38 ha, n = 6; mange β = 0.84 ± 0.33 SE in top core use area model) than foxes without mange ($\bar{x}$ = 13.87 ha, SE = 8.51 ha, n = 27). Mange and breeding status appeared in competing models for home range size (Table 33), but did not show significant directional trends (mange β = 0.29 ± 0.24 SE, breeding status β = -0.12 ± 0.27 SE). Similarly, breeding status and sex appeared in competing models for core use area size (Table 33), but did not show significant directional trends (breeding status β = -0.34 ± 0.34 SE, sex β = 0.24 ± 0.26 SE).

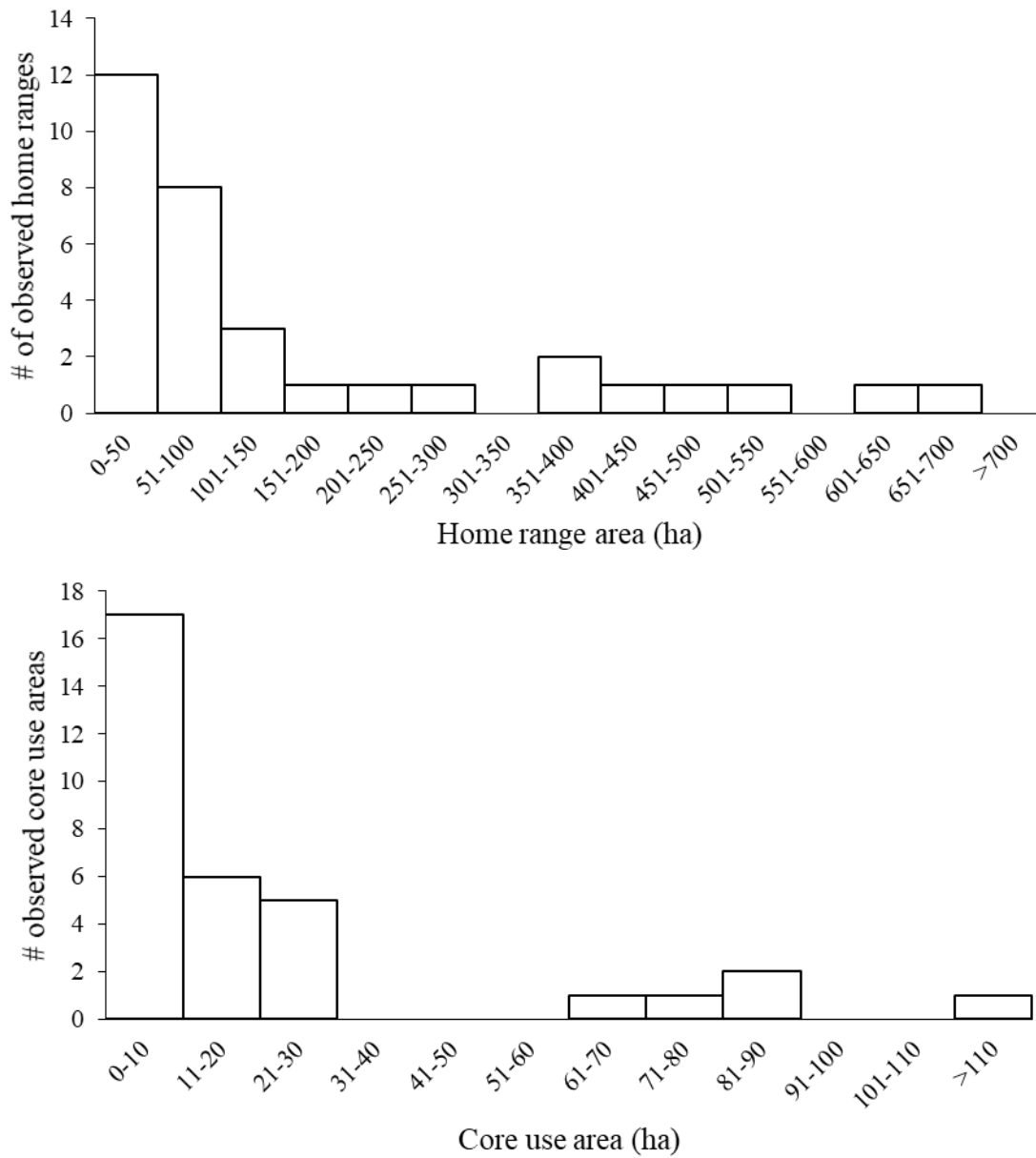


Figure 36. Home range (top) and core use area (bottom) sizes (n=33) estimated for all GPS collared foxes monitored on Fire Island, New York in 2015–2018. 95% and 50% Time Local Convex Hull (T-LoCoH) utilization distribution isopleths were used to represent home ranges and core use areas, respectively.

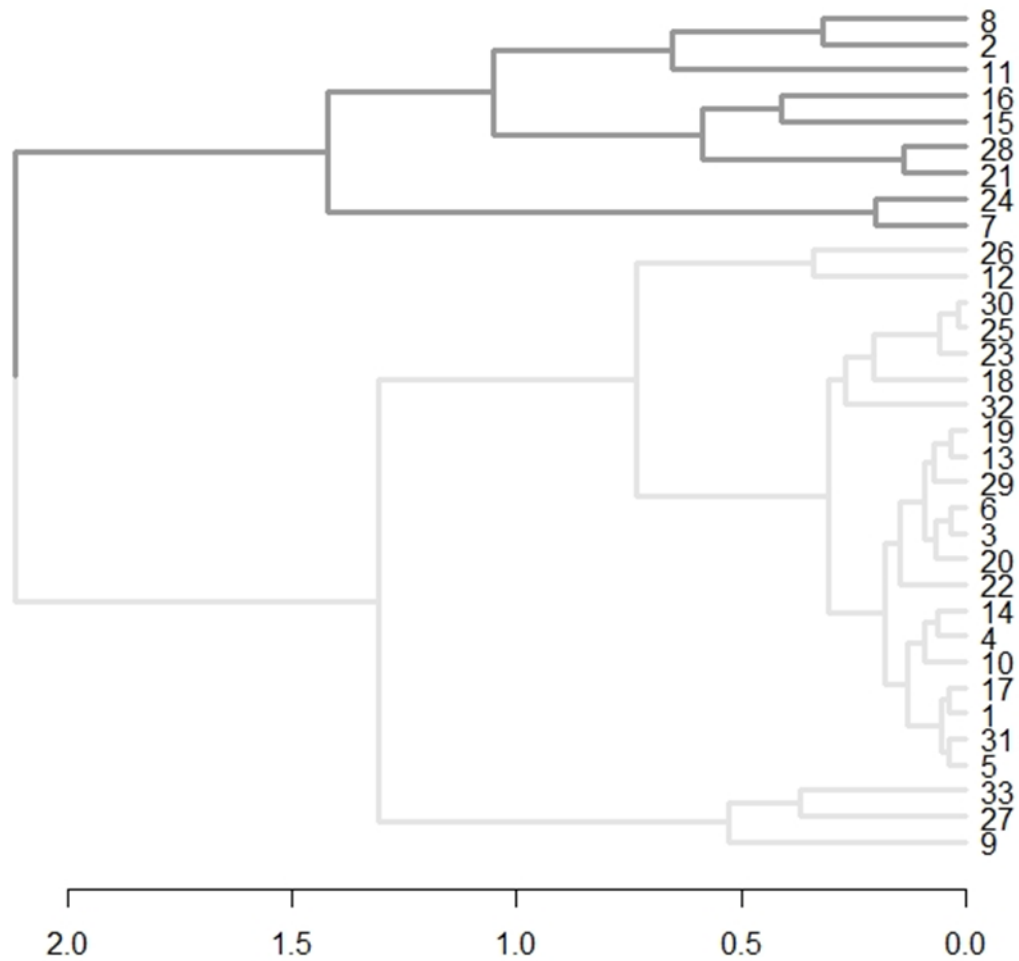


Figure 37. Cluster analysis results used to classify GPS-collared red foxes ($n = 31$ individuals, $n = 33$ unique datasets) monitored on Fire Island, New York in 2015–2018 as either residents or transients, based on similarity in home range size and the coefficient of variation of observed distances to home range centroid. Red foxes with relatively small home ranges and less variation in distance to centroid were classified as residents, while red foxes with relatively large home ranges and high variation in distance to centroid were classified as transients. Two red foxes (M-08 and F-03) were GPS-collared during 2 tracking periods, and thus appear twice in the cluster analysis results.

Table 33. Model selection table for generalized linear mixed model analysis of home range and core use area sizes (n=33) for GPS-collared red foxes monitored on Fire Island, New York in 2015–2018. All models also included animal identity as a random effect. Season = fall/winter versus spring/summer, mange = infected versus not infected, breeding = whether or not that fox was associated with an active breeding den. K = parameter count, AIC_c = Akaike’s Information Criterion corrected for small sample size. Only models within 4 ΔAIC_c of the top model are shown.

Area	Model	K	Log Likelihood	AIC _c	ΔAIC _c	Weight
Home range	Season + Sex	3	-23.78	59.8	0	0.60
	Season + Sex + Mange	4	-23.12	61.5	1.69	0.26
	Season + Sex + Breeding	4	-23.67	62.6	2.79	0.15
Core use area	Mange + Season	3	-25.29	62.8	0.00	0.50
	Mange + Season + Breeding	4	-24.80	64.8	2.02	0.18
	Mange + Season + Sex	4	-24.89	65.0	2.22	0.17
	Season	2	-27.91	65.2	2.44	0.15

Activity patterns and modeling

Residency (whether an animal was resident or transient) was strongly related to both sex (Fisher’s exact test $P = 0.02$) and season ($P = 0.01$), but better explained variation in hourly movement rates than sex or season in preliminary comparisons of univariate models (Table 34). Thus, we dropped sex and season from our modeling of activity patterns and used residency instead. Mean hourly movement rates varied across hours and individuals, ranging from 1.14 m/hr to 1766.61 m/hr ($\bar{x} = 216.33$ m/hr, SE = 8.71 m/hr, n = 787 fox-hr combinations).

Table 34. Model selection table for preliminary comparisons of univariate generalized linear mixed models of hourly movement rates GPS-collared red foxes (n=33) monitored on Fire Island, New York in 2015–2018. All models also included animal identity as a random effect. Residency = resident versus transient, season = fall/winter versus spring/summer, Mange = infected vs. not infected, breeding = whether or not that fox was associated with an active breeding den. K = parameter count, AIC_c = Akaike's Information Criterion corrected for small sample size.

Model	K	Log Likelihood	AIC _c	ΔAIC _c	Weight
Residency	2	-2536.76	5081.6	0	0.95
Sex	2	-2540.01	5088.1	6.52	0.04
Season	2	-2541.56	5091.2	9.61	0.01
Mange	2	-2542.12	5092.3	10.73	0
Breeding	2	-2542.2	5092.4	10.89	0

Hours since sunrise, residency, and mange status most strongly influenced hourly movement rates (Table 35). Mean observed hourly fox movement rates were higher as the number of hours since sunrise increased ($\beta = 8.67 \pm 0.44$ SE and $\beta = 1.29 \pm 0.44$ SE for linear and quadratic effects, respectively). Transient foxes had higher observed mean hourly movement rates across all hours ($\beta = 0.32 \pm 0.08$ SE) compared to residents. Although mange status appeared in the top-ranked model (lowest AIC_c), it did not show clear directional effects ($\beta = 0.15 \pm 0.09$ SE) or substantially improve model fit ($\Delta\text{AIC}_c = 0.24$) over the next best, more parsimonious model, which included only hours since sunrise and residency.

We identified two diel activity categories: a daytime period of relatively low activity (1–9 hours after sunrise; movement rate $\bar{x} = 67.8$ m/hr, SE = 4.41 m/hr) and a nighttime period of relatively high activity (13–22 hours after sunrise; movement rate $\bar{x} = 366.5$ m/hr, SE = 14.8 m/hr). We grouped the hours in between these two periods into a transitional category characterized by moderate but rapidly changing activity levels (all other hours; movement rate $\bar{x} = 184.2$ m/hr, SE = 16.8 m/hr, Figure 38). A post-hoc Kruskal-Wallis test (Kruskal and Wallis 1952) comparing movement rates by diel activity

period suggested that movement rates differed significantly among the 3 periods ($\chi^2_2 = 393.72$, $p < 0.001$), supporting the use of these groupings in further analyses.

Table 35. Model selection table for generalized linear mixed model analysis of hourly movement rates for GPS-collared red foxes (n=33) monitored on Fire Island, New York in 2015–2018. All models also included animal identity as a random effect. Hours = hours since sunrise, residency = resident versus transient, mange = infected versus not infected, breeding = whether or not that fox was associated with an active breeding den. K = parameter count, AIC_c = Akaike's Information Criterion corrected for small sample size. Only models within 4 ΔAIC_c of the top model are shown.

Model	K	Log Likelihood	AIC_c	ΔAIC_c	Weight
Hours + Hours ² + Residency + Mange	5	-2376.77	4767.7	0.00	0.27
Hours + Hours ² + Residency	4	-2377.90	4767.9	0.24	0.24
Hours + Hours ² + Residency + Mange + Breeding	6	-2376.03	4768.2	0.58	0.20
Hours + Hours ² + Residency + Breeding	5	-2377.65	4769.4	1.77	0.11

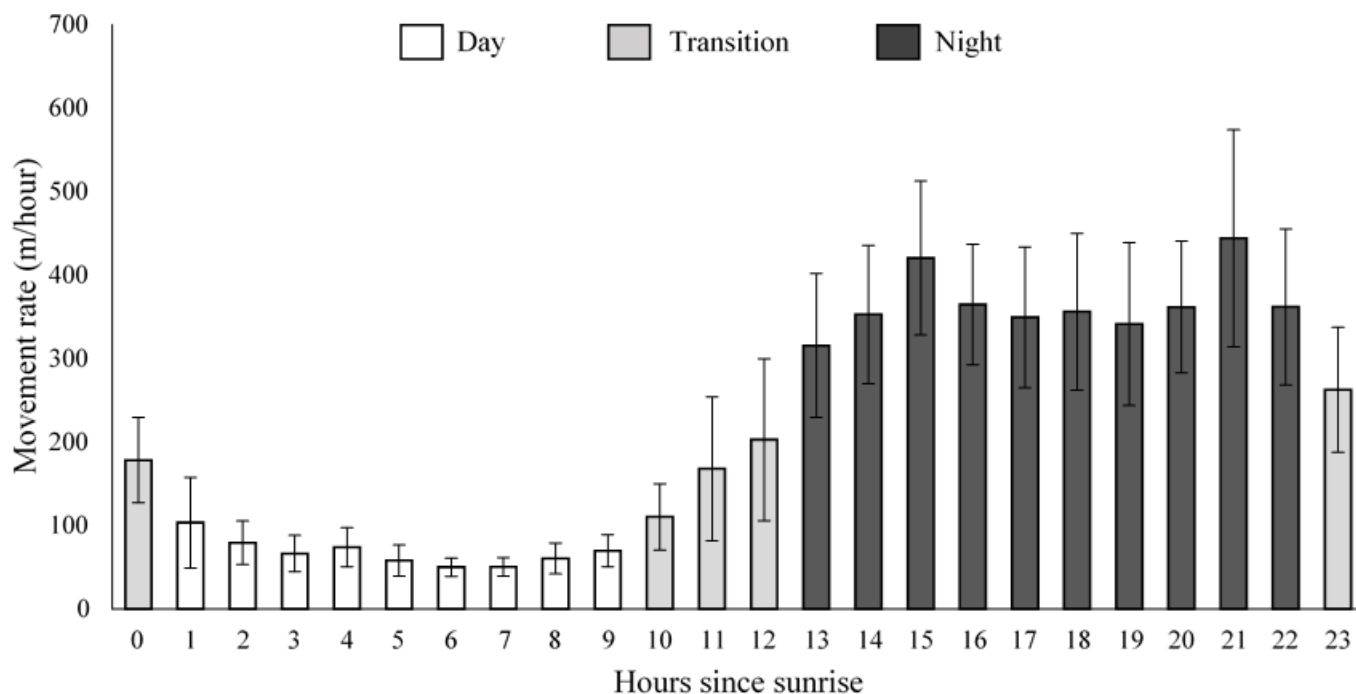


Figure 38. Mean hourly movement rates and 95% confidence intervals (n=33) across all GPS collared red foxes monitored on Fire Island, New York in 2015–2018. We identified 2 diel activity categories based on overlapping confidence intervals among hourly movement rates: a daytime period of low activity (1–9 hours after sunrise), a nighttime period of high activity (13–22 hours after sunrise). We grouped the hours between these 2 periods into a third transitional category.

Within-home range habitat selection

Within-home range (3rd order) habitat selection was most strongly influenced by diel activity period. The top supported model included activity period as an interactive effect with each of the habitat covariates examined; there were no other models with $\Delta AIC_c < 10$ (Table 36). Overall, red foxes used locations that were closer to wet sand, dry sand, and evergreen vegetation than expected and farther from ORV roads and water than expected. Selection for or against vegetation varied among activity periods, and there was no clear selection for or against development (Table 37). During the day, probability of use decreased as distance to vegetation increased ($\beta = -0.66 \pm 0.03$ SE). This pattern held true during transition times relative to daytime ($\beta = 0.43 \pm 0.04$ SE) while at night, probability of use increased, relative to daytime, as distance to vegetation increased ($\beta = 0.79 \pm 0.03$ SE).

SE, Table 37). Of all factors examined, avoidance of ORV roads ($\beta = 0.82 \pm 0.02$ SE) had the strongest effect on probability of use during each activity period.

Table 36. Model selection table for within-home range (3rd order) resource selection function analyses for GPS-collared red foxes (n=33) monitored on Fire Island, New York in 2015–2018. “Habitats” includes the distances to each of the 6 habitat types (development, dry sand, wet sand, evergreen vegetation, other vegetation, water) and one habitat feature (ORV roads) of interest, which were included in all models. All models also included animal ID as a random effect. Activity period = daytime/low activity, nighttime/high activity, or transition hours. Season = fall/winter versus spring/summer, residency = resident versus transient, mange = infected versus not infected, breeding = whether or not that fox was associated with an active breeding den. K = parameter count, AIC_c = Akaike’s Information Criterion corrected for small sample size.

Model	K	Log Likelihood	AIC _c	ΔAIC _c	Weight
Habitats*Activity Period	24	-79718.52	159487.1	0.00	1.00
Habitats*Residency	16	-79830.38	159694.8	207.72	0.00
Habitats*Sex	16	-80406.06	160846.1	1359.07	0.00
Habitats*Breeding	16	-80565.06	161164.1	1677.07	0.00
Habitats*Season	16	-80955.15	161944.3	2457.25	0.00
Habitats*Mange	16	-80977.65	161989.3	2502.26	0.00
Habitats + Activity Period	10	-81107.82	162237.6	2750.59	0.00
Habitats + Sex	9	-81117.47	162254.9	2767.88	0.00
Habitats + Mange	9	-81118.18	162256.4	2769.30	0.00
Habitats + Residency	9	-81118.18	162256.4	2769.31	0.00
Habitats	8	-81119.42	162256.8	2769.80	0.00
Habitats + Breeding	9	-81119.42	162258.8	2771.78	0.00
Habitats + Season	9	-81119.42	162258.8	2771.80	0.00

Table 37. Standardized beta coefficient estimates, standard errors, and 95% confidence intervals from the top supported mixed effects logistic regression model of within-home range (3rd order) resource selection by GPS-collared red foxes (n=33) monitored on Fire Island, New York in 2015–2018. Animal identity was also included in the model as a random effect. Negative values indicate selection for areas closer to a given habitat type than expected, while positive values indicate selection for areas further from a given habitat type than expected. Confidence intervals overlapping zero indicate no clear directional selection pattern. * indicates confidence intervals that do not overlap zero.

Covariate	Estimate	SE	Lower CI	Upper CI
Intercept ^{a*}	-1.96	0.12	-2.20	-1.72
Period (night)*	0.10	0.02	0.07	0.14
Period (transition)*	0.10	0.02	0.06	0.14
Distance to ORV road*	0.82	0.02	0.78	0.85
Distance to development	-0.02	0.02	-0.05	0.01
Distance to dry sand*	-0.31	0.02	-0.35	-0.27
Distance to wet sand*	-0.54	0.03	-0.59	-0.49
Distance to evergreen vegetation*	-0.17	0.02	-0.20	-0.14
Distance to other vegetation*	-0.66	0.03	-0.71	-0.60
Distance to water*	0.67	0.02	0.62	0.71
Period (night) × Distance to ORV road ^b	-0.02	0.02	-0.06	0.01
Period (transition) × Distance to ORV road	0.01	0.02	-0.03	0.05
Period (night) × Distance to development	-0.04	0.02	-0.08	0.00
Period (transition) × Distance to development	0.01	0.02	-0.03	0.06
Period (night) × Distance to dry sand*	-0.41	0.03	-0.47	-0.35
Period (transition) × Distance to dry sand*	-0.28	0.04	-0.35	-0.21
Period (night) × Distance to wet sand*	0.23	0.03	0.17	0.30
Period (transition) × Distance to wet sand*	0.27	0.04	0.20	0.35
Period (night) × Distance to evergreen vegetation*	0.08	0.02	0.04	0.12
Period (transition) × Distance to evergreen vegetation	0.04	0.03	-0.01	0.09
Period (night) × Distance to other vegetation*	0.79	0.03	0.73	0.85
Period (transition) × Distance to other vegetation*	0.43	0.04	0.35	0.50
Period (night) × Distance to water*	-0.65	0.03	-0.70	-0.60
Period (transition) × Distance to water*	-0.25	0.03	-0.31	-0.19

^aUsing period (day) as the reference level for intercept and main effects

^b × indicates an interaction with the main effect. Total effect = main effect + interaction.

Landscape-scale habitat selection of red foxes

Landscape-scale (2nd order) selection was strongly influenced by sex. The top supported model included sex as an interactive effect with each of the habitat covariates examined; there were no other models with $\Delta AIC_c < 10$ (Table 38). Selection patterns differed for some, but not all, habitat types by sex, with selection for or against dry sand and ORV roads driving landscape-scale habitat selection (Table 39). Both sexes selected for areas that were closer to dry sand ($\beta = -1.07 \pm 0.04$ SE, main effect; $\beta = -0.12 \pm 0.06$ SE, interactive effect of sex) and non-evergreen vegetation than expected based on availability ($\beta = -0.42 \pm 0.03$ SE, main effect; $\beta = 0.04 \pm 0.05$ SE, interactive effect of sex), but did not show significant selection for or against development. Female foxes selected for areas that were farther from ORV roads than expected ($\beta = 1.45 \pm 0.04$ SE), while male foxes selected for areas closer to these roads ($\beta = -2.32 \pm 0.06$ SE). Female foxes selected for areas closer to wet sand ($\beta = -0.61 \pm 0.04$ SE) and evergreen vegetation ($\beta = -0.44 \pm 0.03$ SE) and farther from water ($\beta = 0.45 \pm 0.03$ SE) than expected, while male foxes did not show statistically significant selection for or against these habitat types. To illustrate these selection patterns, maps of resident red fox home ranges within a single monitoring area overlaid onto 2016 landcover classification data are shown in Figure 39 as examples. Maps of residential red fox home ranges for all monitoring areas in 2016 and 2017 overlaid onto that year's landcover classification data are included in the online Supporting Information (Figure 40, Figure 41, Figure 42, Figure 43).

Table 38. Model selection table for landscape-scale (2nd order) resource selection function analyses for GPS-collared red foxes (n=21) monitored on Fire Island, New York in 2016–2017. “Habitats” includes the distances to the 6 habitat types (Development, dry sand, wet sand, evergreen, other vegetation, water) and one habitat feature (ORV roads) of interest, which were included in all models. All models also included animal ID as a random effect. Residency = resident versus transient, mange = infected versus not infected, breeding = whether or not that fox was associated with an active breeding den. K = parameter count, AIC_c = Akaike’s Information Criterion corrected for small sample size.

Model	K	Log Likelihood	AIC _c	ΔAIC _c	Weight
Habitats*Sex	16	-28816.07	57666.2	0.00	1.00
Habitats*Mange	16	-29746.89	59527.8	1861.64	0.00
Habitats*Breeding	16	-29824.97	59684.0	2017.80	0.00
Habitats*Residency	16	-29990.36	60014.7	2348.58	0.00
Habitats + Sex	9	-30063.26	60146.5	2480.37	0.00
Habitats	8	-30064.76	60147.5	2481.37	0.00
Habitats + Residency	9	-30063.80	60147.6	2491.44	0.00
Habitats + Mange	9	-30063.84	60147.7	2481.52	0.00
Habitats + Breeding	9	-30064.56	60149.1	2482.98	0.00

Table 39. Standardized beta coefficient estimates and 95% confidence intervals from the top supported mixed effects logistic regression model of landscape-level (2nd order) resource selection by GPS-collared red foxes (n=21) monitored on Fire Island, New York in 2016–2017. Animal identity was also included in the model as a random effect. Negative values indicate selection for areas closer to a given habitat type than expected, while positive values indicate selection for areas further from a given habitat type than expected. Confidence intervals overlapping zero indicate no clear directional selection pattern. * indicates confidence intervals that do not overlap zero.

Covariate	Estimate	SE	Lower CI	Upper CI
Intercept ^{a*}	-2.27	0.30	-2.86	-1.68
Sex (male)	0.16	0.45	-0.72	1.04
Distance to ORV road*	1.45	0.04	1.38	1.53
Distance to development	0.03	0.02	-0.01	0.08
Distance to dry sand*	-1.07	0.04	-1.15	-0.99
Distance to wet sand*	-0.61	0.04	-0.68	-0.54
Distance to evergreen vegetation*	-0.44	0.03	-0.49	-0.39
Distance to other vegetation*	-0.42	0.03	-0.48	-0.36
Distance to water*	0.45	0.03	0.39	0.51
Sex (male) × Distance to ORV road ^{b*}	-2.32	0.06	-2.44	-2.21
Sex (male) × Distance to development*	-0.08	0.03	-0.15	-0.02

Sex (male) × Distance to dry sand	-0.12	0.06	-0.24	0.00
Sex (male) × Distance to wet sand*	0.68	0.05	0.59	0.77
Sex (male) × Distance to evergreen vegetation*	0.39	0.04	0.32	0.47
Sex (male) × Distance to other vegetation	0.04	0.05	-0.06	0.14
Sex (male) × Distance to water*	-0.51	0.04	-0.58	-0.43

^aUsing sex (female) as the reference level for intercept and main effects

^b × indicates an interaction with the main effect. Total effect = main effect + interaction.

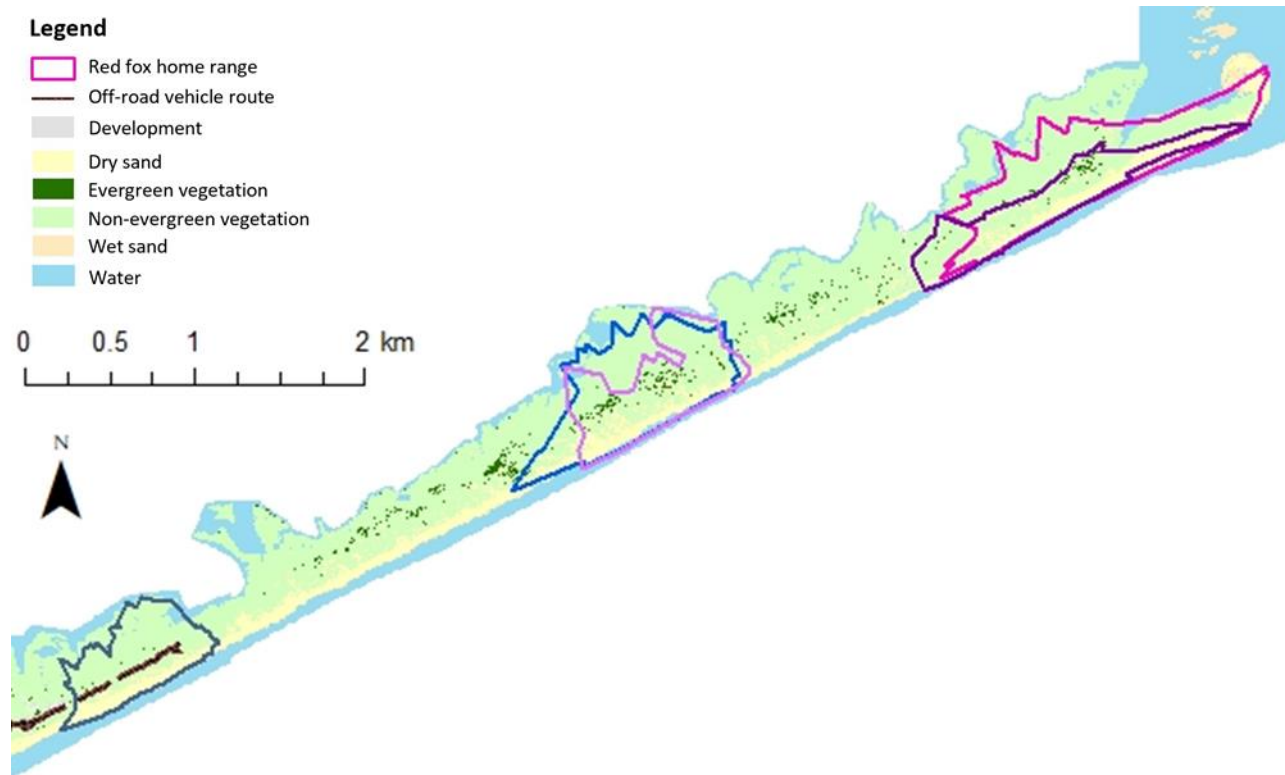


Figure 39. Home ranges of resident red foxes ($n = 5$; F-08, F-09, F-10, M-13, and M-14) that were monitored at Fire Island National Seashore in 2016, overlaid onto 2016 landcover classification data. 95% Time Local Convex Hull (T-LoCoH) utilization distribution isopleths were used to represent home ranges.

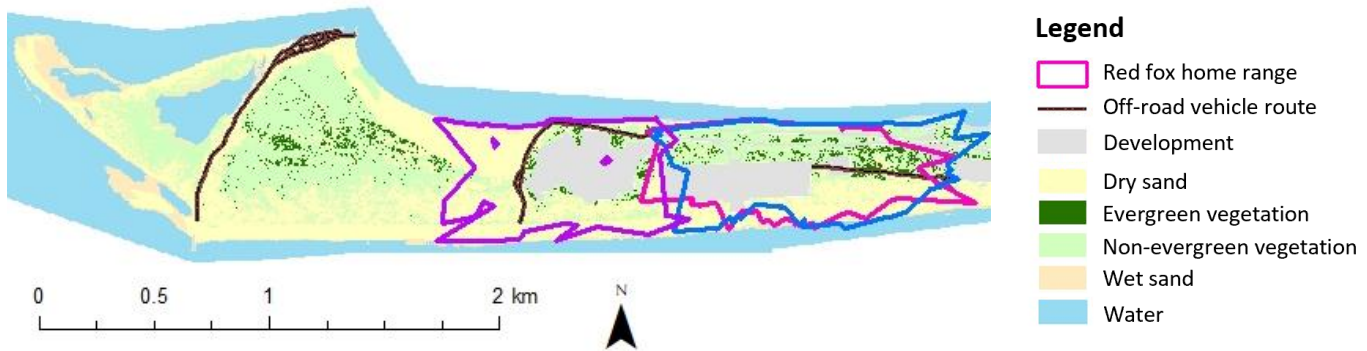


Figure 40. Home ranges of resident red foxes ($n = 3$; F-05, F-07, and M-08) that were monitored at Robert Moses State Park in 2016, overlaid onto 2016 landcover classification data. 95% Time Local Convex Hull (T-LoCoH) utilization distribution isopleths were used to represent home ranges.

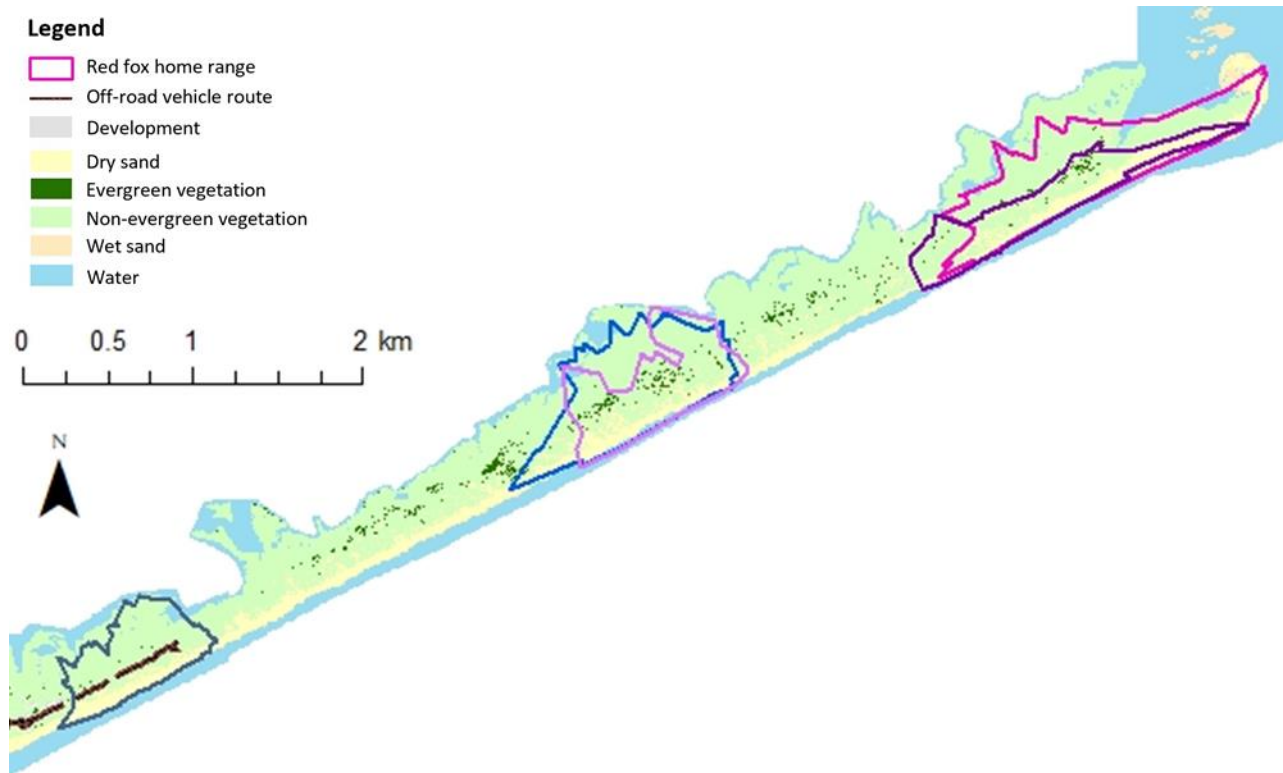


Figure 41. Home ranges of resident foxes ($n = 5$; F-08, F-09, F-10, M-13, and M-14) that were monitored at Fire Island National Seashore in 2016, overlaid onto 2016 landcover classification data. 95% Time Local Convex Hull (T-LoCoH) utilization distribution isopleths were used to represent home ranges.

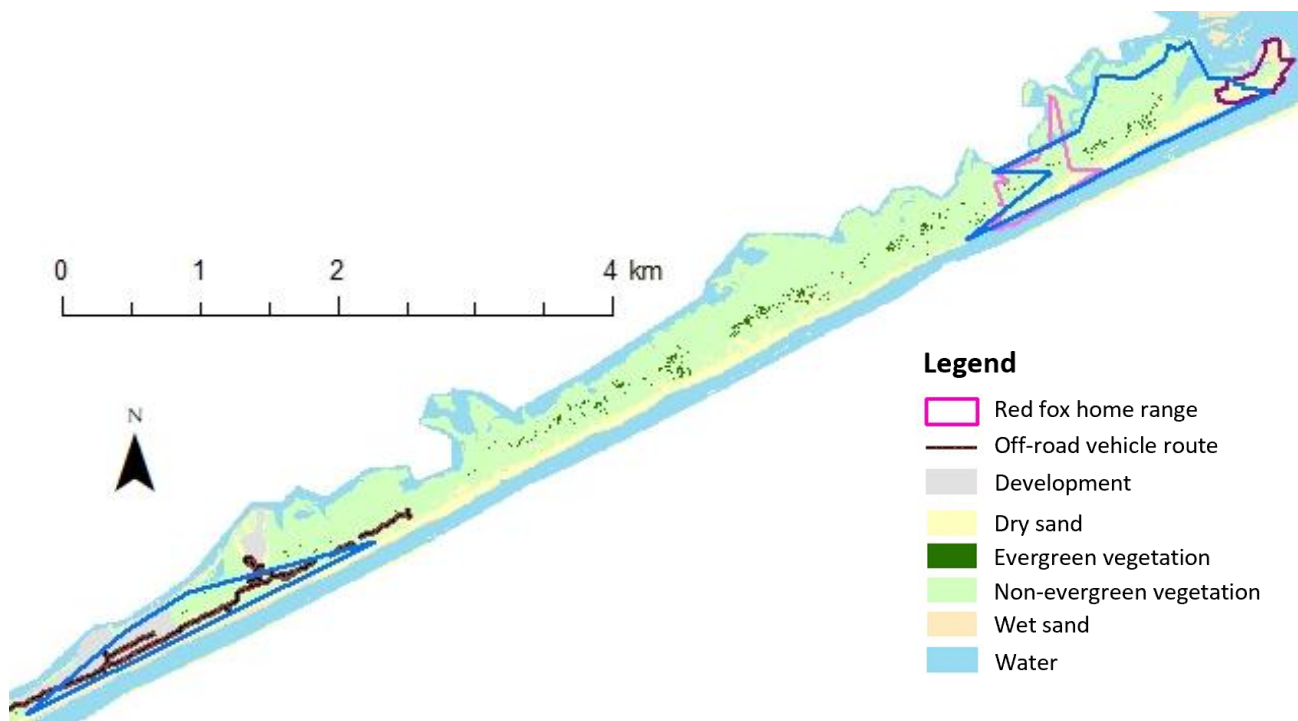


Figure 42. Home ranges of resident red foxes ($n = 3$; F-14, F-15, and M-18) that were monitored at Fire Island National Seashore in 2017, overlaid onto 2017 landcover classification data. 95% Time Local Convex Hull (T-LoCoH) utilization distribution isopleths were used to represent home ranges.

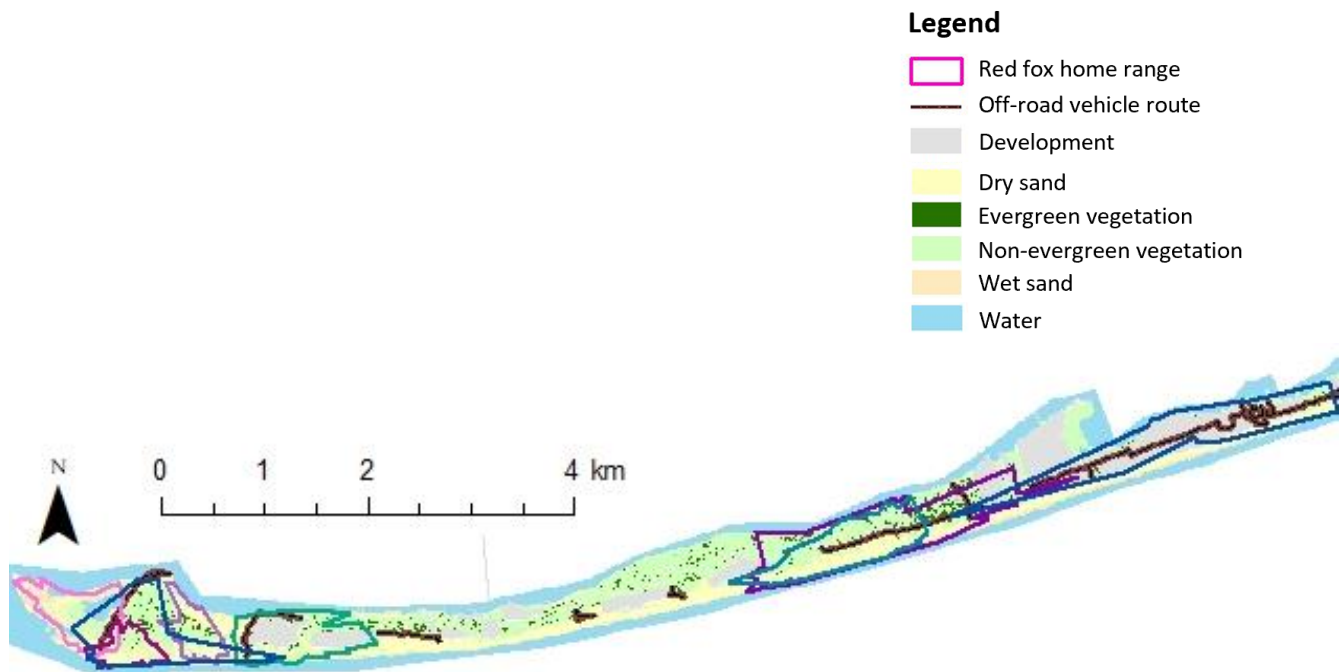


Figure 43. Home ranges of resident red foxes ($n = 7$; F-03, F-11, F-12, F-13, M-08, M-15, and M-17) that were monitored at Robert Moses State Park and the Fire Island Lighthouse Tract in 2017, overlaid onto 2017 landcover classification data. 95% Time Local Convex Hull (T-LoCoH) utilization distribution isopleths were used to represent home ranges.

Island-wide habitat suitability predictions for red foxes

Based on the results of our 2nd order, landscape-level resource selection function analyses, we created relative habitat suitability maps for males and females within the study area. Predictive accuracy varied among each of these maps and by the number of predictive bins used, and was consistently higher using 5 predictive bins compared to 10 predictive bins, averaging 0.83 and 0.75, respectively, across all mapped years and sexes (Table 40).

Table 40. Predictive accuracy of habitat suitability models for red foxes on Fire Island, New York in 2016-2017 for each map created, and averages across all maps, using either 10 or 5 predictive bins.

Year	Sex	10 bins	5 bins
2016	Male	0.73	0.85
2016	Female	0.72	0.87
2017	Male	0.65	0.66
2017	Female	0.91	0.93
Average Predictive Accuracy		0.75	0.83

A closer examination of predicted habitat suitability (Figure 44) and mean suitability values within the restoration areas at Smith Point County Park (Table 41), calculated by averaging the suitability values for all pixels within each restoration area boundary, shows variable suitability between the sexes and between the 2 areas. Within these areas, predicted suitability was higher for both sexes in New Made compared to Great Gun, with a mean suitability score of 3.47 and 3.14 (out of 5), respectively, across years and sexes. At Great Gun, suitability was consistently highest along the main dune and in areas closer to vegetation. At New Made, suitability was highest closer to vegetated and wet sand edges, but varied more widely between sexes and years.

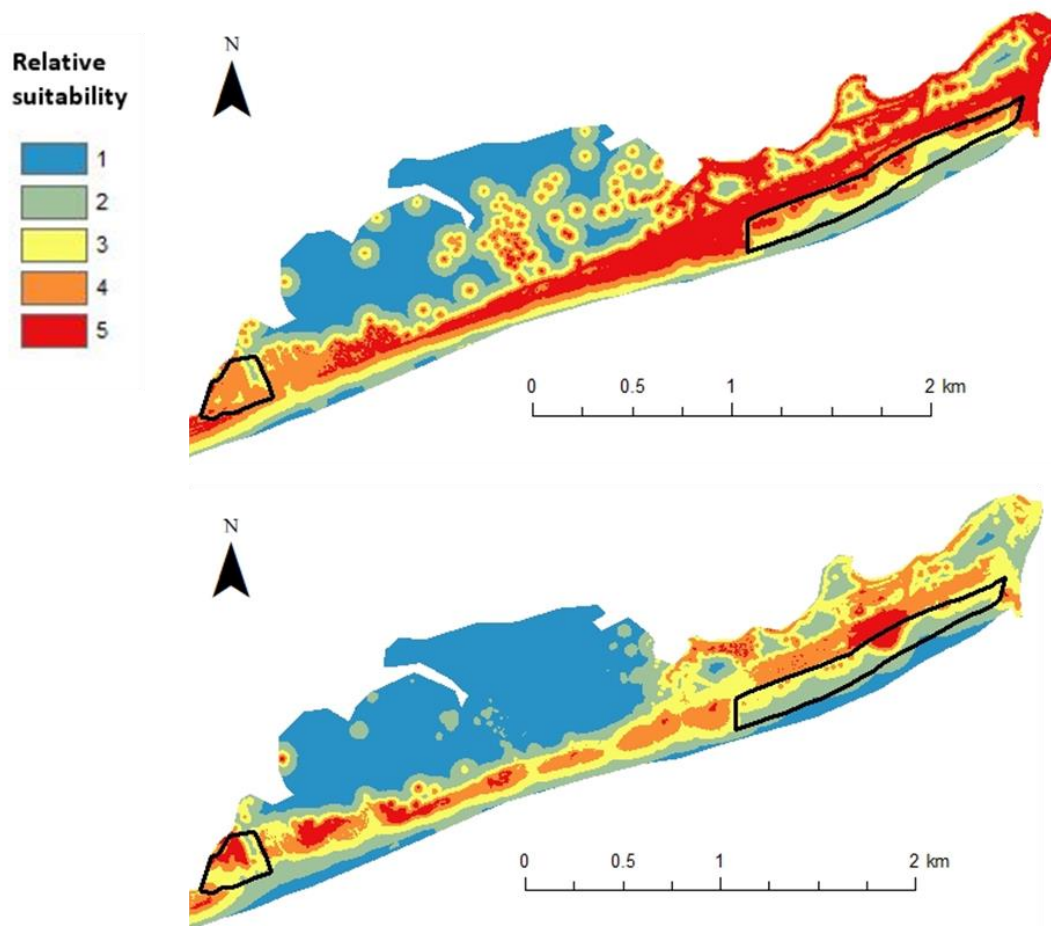


Figure 44. Predicted habitat suitability (5 = highest suitability to 1 = lowest suitability) maps for male (top) and female (bottom) red foxes within the USACE restoration areas (outlined in black) at Smith Point County Park, using 2017 landcover classification data.

Table 41. Mean predicted habitat suitability scores (5 = highest suitability to 1 = lowest suitability) for red foxes within the USACE restoration areas at Smith Point County Park on Fire Island, New York in 2016–2017. Mean predicted habitat suitability scores were calculated by averaging the suitability values for all pixels within each restoration area boundary.

Sex	Year	Great Gun	New Made
Male	2016	3.55	3.64
Female	2016	2.71	2.86
Male	2017	3.54	3.77
Female	2017	2.76	3.62
Average Suitability		3.14	3.47

Discussion

The estimated red fox home range and core use area sizes reported in this study are on the lower end of what has been reported in previous studies. We observed home range sizes ranging from ~10 ha to ~659 ha and averaging 164.44 ± 33.31 ha. In comparison, home ranges sizes ranging from ~10 ha to >5,000 ha have been previously reported for individual red foxes (Lucherini and Lovari 1996, Macdonald 1987, Voight 1987), with mean home range size estimates within studies ranging from 18 ha in urban England (Baker et al. 1998, Baker et al. 2000) to > 1600 ha in the Canadian tundra (Jones and Theberge 1982, Baker and Harris 2004). Comparative studies of red fox home range sizes have suggested that habitat type, habitat richness, relative food availability, and resource distribution influence home range size (Lucherini and Lovari 1996, Goszczyński 2002, Macdonald et al. 2004).

Previous studies in coastal habitats have reported home range sizes similar to those reported in this study. Dekker et al (2001) observed home ranges from <50 ha to 650 ha in Dutch coastal dune habitat, with about half of home ranges < 100 ha. In Dutch wet coastal grasslands, mean home ranges varied from 253-314 ha, depending on the estimation method used (Meisner et al. 2014). In coastal Australia, Meek and Saunders (2000) observed home ranges from 60-270 ha, with a mean of 135 ha. Another study in coastal Australia reported larger home ranges of 120-520 ha (Phillips and Catling 1991), possibly due to differences in estimation methods. These results suggest that red fox home range sizes in coastal habitats fall on the lower end of reported red fox home range sizes. This also appears to be the case in coastal habitats on islands. For example, Silva et al. (2009) reported red fox home ranges between 77 and 168 ha, depending on estimation method used, on Prince Edward Island, with an average 95% fixed-kernel area of 102.3 ha ($n = 3$ foxes). In the only previous study to examine red fox home range sizes on a barrier island, Brittinger (1993) reported a mean home range of juvenile red foxes ($n = 3$) of $106.39 \text{ ha} \pm 14.63 \text{ ha (SE)}$ and a range of ~90-135 ha for foxes monitored in June–September on Assateague Island. While our mean estimated home range size for foxes monitored from April–August ($115.30 \text{ ha} \pm 34.12 \text{ ha SE}$) was similar to their estimate, we observed much more variation, likely due to our larger sample size and monitoring of both resident

and transient adults. The use of GPS collars in this study vs. VHF collars in this study could have also contributed to this difference in estimates, as long distance movements may be more difficult to detect using VHF radio telemetry, which relies on the observer being close enough to the target animal to pick up the collar's radio signal.

The observed transient behavior of a significant proportion of GPS-collared male red foxes suggests that a subset of red foxes on the island are regularly moving between the parks and/or private communities. Several of these transient animals routinely traveled the entire length of the island available to them (without crossing Old Inlet or the 2 motor vehicle bridges connecting Fire Island to mainland Long Island). The fact that we did not observe any red foxes crossing Old Inlet during the study indicates that this inlet was likely a barrier to red fox movement between the eastern and western portions of the island. In the context of predation management, this suggests that any activities aimed at reducing fox distribution or abundance should be coordinated across management areas. It also suggests a high probability that any territories that become vacant, either from removal or natural mortality, could be quickly recolonized.

The observed differences in hourly movement rates suggest differing temporal patterns of predation risk for piping plovers throughout the day, as red foxes were relatively inactive until ~10 hours after sunrise. Red foxes are generally nocturnal-crepuscular, but may strategically shift activity patterns in response to factors including prey activity, human disturbance, and seasonal changes (Doncaster and Macdonald 1997, Díaz-Ruiz et al. 2016). For example, red fox activity patterns in areas of low human disturbance in central Spain were correlated with diurnal prey activity patterns, while red foxes in more urban areas were less active during the day despite diurnal prey activity Díaz-Ruiz et al. (2016). The observed nocturnal-crepuscular activity patterns in our study area could be related to the high amount of human disturbance, but could be explained by other factors as well. We did not examine prey activity patterns in our study or compare red fox activity patterns or movement rates in low human use vs. high human use areas.

Considered alongside the observed activity pattern results, the observed difference in red fox selection for or against vegetation based on time of day suggests differential habitat use for different activities. Red foxes on the island appear to be selecting areas closer to vegetation and wet sand for daytime resting periods, and selecting less vegetated habitats for nighttime periods of higher activity and movement. Previous studies suggest that red fox habitat preferences vary widely with the available habitat and geographic location (Ables 1983, Soulsbury et al. 2010). In general, studies suggest that red foxes tend to use locations with a variety of vegetation types, but avoid large continuous areas of only one habitat type. These patchwork areas likely offer an ideal combination of food and cover (Ables 1983, Voigt 1987). The habitat selection patterns observed in this study support the idea of selection for edge and patchy areas. On Assateague Island, Krim et al. (1990) examined red fox den site selection, reporting that dens were most frequently located in shrub/early successional and dune habitats. Stantial et al. (2020) found that red foxes on barrier islands in southern New Jersey were more likely to use areas closer to dunes, based on track surveys and occupancy modeling. Gieder (2015) examined red fox occupancy patterns on Assateague Island using remote cameras, but did not find any significant habitat relationships.

The results of this study are also in agreement with previous studies of red foxes in non-barrier island coastal habitats that suggest a general preference for dry land over wet habitats. For example, red foxes on Prince Edward Island used dunes and fields more often than expected and used forest, marsh, and water less often than expected based on availability (Silva et al. 2009). Similarly, red foxes in coastal Denmark used dry habitats, such as fields, more often than expected and used wet habitats, such as wetlands and ditches less often than expected based on availability (Meisner et al. 2014). However, we observed differing patterns of selection regarding roads and development than did Silva et al. (2009). We observed strong avoidance of ORV roads within home ranges, while Silva et al. (2009) observed selection for areas of human use and either selection for or no preference for roads, depending on site. For comparison, Stantial et al. (2020) found that proximity to human development

had very minimal effect on probability of red fox habitat use. This suggests that, while coastal red foxes in general prefer dry habitats, selection for anthropogenic features may differ by location. We observed several differences between within-home range and landscape-scale habitat selection, suggesting that foxes on the island are selecting for different features at different spatial scales. Much of the literature on red fox habitat selection is focused on within-home range habitat selection; we found only one previous study of landscape-scale red fox habitat selection in a comparable environment. In addition to the telemetry results described above, Silva et al. (2009) used snow tracking to investigate 2nd order red fox habitat selection on Prince Edward Island, and found that foxes selected for dune, shrub, and developed habitats and against forest compared to available habitats, as they did within their home ranges. Foxes within Prince Edward Island National Park also selected against water, but those outside of the park did not show any pattern of selection for or against it.

In this study, the strong avoidance of ORV roads observed within home ranges was not consistent at the landscape scale, with males selecting for areas closer to ORV roads while females avoided those areas, suggesting that spatial scale as well as sex may influence perceived risk and habitat preferences. The observed difference in selection among sexes could reflect differing tolerance for the risks associated with ORV roads, or could be a result of differing factors driving home range selection. For example, females may select for areas of optimal habitat quality for denning and kit-rearing, while males may select for areas that maximize available food resources or travel efficiency for maintaining territorial markings. Hinton et al. (2015) found similar differences in selection for vs. against roads in transient coyotes compared to residents, and hypothesized that either more efficient movement paths or increased ability to detect residential animals and their territory boundaries could explain this difference in selection.

The relative suitability maps produced here can be used to predict relative predation risk across the landscape and to identify areas where predator management efforts should be focused. Visual examination of these suitability maps and the maps of red fox home ranges overlaid onto the

underlying landcover classification data highlights the influence of ORV roads on the resulting suitability predictions for each sex. Because ORV roads spanned much of the island, areas of high suitability for females were limited. Across the sexes, these maps also highlight the importance of vegetation management, particularly in areas known to be used by plovers. Close inspection of the maps shows that areas of higher relative suitability for red foxes align closely with the distribution of vegetation and evergreen habitat on the island. Vegetation can be managed to decrease relative suitability for red foxes. Specifically, vegetation removal can decrease daytime resting sites and hunting concealment cover for red foxes, while also increasing the amount of open sandy beach area, which piping plovers on Atlantic barrier islands prefer for nesting habitat (Cohen et al. 2008, Walker et al. 2019). Such vegetation removal could also improve the effectiveness of the restoration areas, particularly New Made, by improving overall nesting suitability.

Mange influenced some but not all aspects of red fox spatial ecology on the island, with affected red foxes using larger core use areas compared to unaffected red foxes. This suggests that affected red foxes may be covering more area and expending more energy. Although we did not observe any differences between affected and unaffected fox habitat selection patterns, previous research suggests that mange may also influence red fox habitat selection. Red foxes suffering from advanced stages of mange in southeastern Norway used areas closer to developed areas compared to unaffected foxes, potentially due to increased reliance on anthropogenic food subsidies as their ability to hunt decreased with declining health (Carricondo-Sanchez et al. 2017). In addition, mange-related declines in red fox population density also may influence spatial ecology, with remaining red foxes expanding their use areas as formerly occupied territories are vacated. Red fox home range sizes in Bristol, UK, were relatively small prior to a mange epizootic, when population densities were relatively high, but expanded significantly following the epizootic, when population densities were relatively low (Baker et al. 2000, Soulsbury et al. 2010). In that study, it took several years for home ranges sizes and population densities to return to pre-outbreak levels (Soulsbury et al. 2007). We observed substantial declines in red fox population density on Fire Island following sarcoptic mange

outbreaks (*Chapter 2*, Robertson et al. 2019), but were limited in our ability to compare home range sizes pre- vs. post-mange by the lack of GPS-collared red foxes east of Old Inlet following the mange outbreak in that portion of the study area, and the end of data collection prior to the end of the outbreak west of Old Inlet. Thus, home range sizes among red foxes currently inhabiting the study area may be larger than expected based on this study, but should stabilize over time as population density returns to pre-mange levels.

Management implications

The observed long-range movements of several red foxes and high proportion of transient individuals in the population suggest a high capacity for recolonization should territories become vacant. Thus, lethal removal activities aimed at reducing red fox distribution and abundance in shorebird nesting areas are unlikely to be effective in the long term. Instead, park resources may be better used to manage vegetation, which will reduce habitat suitability for red foxes while improving suitability for shorebird nesting (Robinson 2020). Our findings also highlight the need for any future predator management activities in our study area to be coordinated across the entire island, as transient foxes traveled regularly between management units and private property. The observed nocturnal activity pattern of red foxes suggests that predation risk for shorebirds is likely highest overnight, and highlights the importance of diel timing for predation mitigation efforts. In the future, the relative habitat suitability maps resulting from our analyses could be compared to similar habitat suitability maps for piping plovers to identify areas of high predation risk on the island where areas of high relative red fox and piping plover suitability overlap, allowing managers to prioritize these areas for vegetation and predation management activities.

Section 3: Quantify the interactions of red fox with shorebird nests and chicks before and during the recovery from the mange outbreak. Monitor the impacts of foxes versus other predators on plover nests and chicks.

This section describes data collection, analytical methods, and results related to the following objective for red fox monitoring associated with the Fire Island Inlet to Moriches Inlet Fire Island Stabilization Project during the 2015-2020 monitoring period. We were not able to collect additional field data in 2020 due to covid-19 restrictions.

Objective 5: Quantify the interactions of red foxes with shorebird nests and chicks.

Based on the two very different types of data and analyses used to address Objective 5, we have split our summary of monitoring activities and results for this objective into two sections. This section describes the use of spatial data to examine spatial interactions between red foxes and piping plover nests. The next section, Part 3, Section 4, describes the use of fecal dietary analyses and prey items surveys at dens to examine direct predatory interactions between red foxes and piping plover chicks and adults.

Introduction

Predation management is a component of recovery efforts for many threatened and endangered species (Engeman et al. 2009). For the federally threatened piping plover (*Charadrius melodus*) and other shorebirds breeding on the U.S. Atlantic coast, predation has been identified as one of several factors that may be limiting population growth (USFWS 1996, Hunt et al. 2019a). Consequently, managers frequently seek to reduce predation of nests, chicks, and adults using various lethal and non-lethal management strategies (Hecht and Melvin 2009, Cohen et al. 2016, Darrah et al. 2020).

Nest exclosures are one type of non-lethal management strategy aimed at preventing nest predation by surrounding the nest with wire mesh fencing, creating a physical barrier between the nest and potential predators (Rimmer and Deblinger 1990, Melvin et al. 1992). The species of

protection interest, such as piping plovers, can easily fit through the gaps in between the rows and columns of wires that form the fencing, while larger animals generally cannot. Empirical comparisons of nest predation rates at exclosed and unexclosed nests suggest that these exclosures can be effective in reducing nest predation and increasing hatch success (Maslo and Lockwood 2009, Barber et al. 2010, Dinsmore et al. 2014, Cohen et al. 2016). Nest exclosures may be less effective in increasing overall reproductive output, as they do not influence post-hatch survival of precocial chicks once they leave the exclosed area (Neuman et al. 2004, Cohen et al. 2009).

Despite the potential benefits of nest exclosures, there are concerns over whether these conspicuous structures might attract predators to nest sites. Visual cues are more likely to elicit responses from red foxes than olfactory cues under certain light conditions, including at twilight when foxes often forage (Österholm 1964). Object size may also influence whether predators investigate or avoid novel objects, with more frequent neophobic responses to larger objects (Heffernan et al. 2007, Windberg 2011). If exclosures do attract predators to nests, the possibility of increased parental abandonment, predation of adults, or predation of chicks immediately after hatching could negate the potential benefits of reduced nest predation associated with exclosure use (Neuman et al. 2004, Barber et al. 2010, Beaulieu et al. 2014, Dinsmore et al. 2014, Cohen et al. 2016).

Once a red fox has located an exclosed nest, there is evidence that they may sometimes learn how to penetrate the exclosure by digging underneath or climbing into it, rendering these barriers ineffective unless modifications, such as rigid wire tops or secondary electric barriers, are put in place. Cohen et al. (2009) observed red fox predation at 22.9% of exclosed nests during their study on Westhampton Island, New York, and Barber et al. (2010) reported red fox predation at 2 exclosed nests in Prince Edward Island National Park, Canada. Similar issues have been reported with red foxes entering exclosures used to protect ground-nesting ducks, despite the use of electric wires in those exclosures (West et al. 2007).

There are also concerns over whether the hatching process itself may attract predators to nest. Prior to hatching, chicks use an egg tooth to begin fracturing the egg shell. This pipping process may

last from a few hours up to a few days, depending on the species of bird, until they have fully penetrated the shell and can emerge. During this time, the chicks will vocalize inside the egg (Gottlieb and Vandenburg 1968, Freeman and Vince 1974, Kostoglou et al. 2017). These vocalizations, or the parental behaviors that they may elicit, could potentially assist predators in locating nests. Kostoglou et al. (2017) found no difference in nest survival at unexclosed artificial red-capped plover (*Charadrius ruficapillus*) nests where recorded pre-hatch vocalizations were played versus nests without these playbacks, suggesting that auditory cues alone are unlikely to attract red foxes and other nest predators. However, it is unknown whether pipping might impact predator behavior when considered in combination with exclosure use.

Further information on red fox behavioral responses to nest exclosures and hatching is needed to inform predation management. Previous research on predator responses to exclosures has been limited to the use of remote cameras at nests and an artificial nest experiment (Beaulieu et al. 2014). In that study, Beaulieu et al. (2014) found that red foxes and avian predators visited exclosed piping plover nests more frequently than unexclosed nests, and that red fox visits at exclosed nests were significantly longer than those at unexclosed nests.

Our goal was to use GPS collar data from red foxes to determine whether these potential predators were attracted to nest exclosures for piping plovers, either upon exclosure setup at nests or during pipping and hatching. We compared the mean distances from individual red fox locations to piping plover nests within that red fox's home range before vs. after exclosure setup and plover hatching events. In order to cause a shift in mean distances from their locations to nests, red foxes would have had to consistently use locations closer to nests over an extended time period. However, there also was the possibility that red foxes could have been keying on exclosures or hatching events over shorter time periods or smaller spatial scales, which may not have been reflected in their mean distances. Thus, we also tested for changes in the proportion of red fox locations within 100 m of exclosures before vs. after these events. We hypothesized that red foxes would be attracted to the visual cues of nest exclosures in their home range and that locations would be closer to nests on

average, and/or a greater proportion of locations would be within the 100-m buffer zone, after exclosure setup, egg-pipping, and hatching than before.

Methods

Red Fox Trapping, GPS Collaring, and Tracking

We used Victor 1 ½ Soft Catch and Bridger #2 padded foothold traps to capture red foxes in the study area during April–May 2016 and February–April of 2017, following the Association of Fish and Wildlife Agencies’ Best Management Practices for Trapping Red Foxes in the United States (AFWA 2014). We focused our trapping efforts in and around known piping plover nesting areas, based on previous years’ data from concurrent shorebird monitoring activities (Walker et al. 2019, C.C. Robertson et al., Virginia Tech, unpublished report).

We outfitted captured red foxes with GPS collars (Quantum 4000E, medium size; Telemetry Solutions, Concord, CA). These collars were programmed to record locations once every 1–2 hours on every day from April 20th through the end of May, then once every 2 hours, on every other day until programmed collar drop-off in early August. Every 10–14 days after deployment, we located collared red foxes via radio telemetry tracking of the collar’s VHF signal and approached to within 200m to connect wirelessly to the collar and download data using a UHF antenna, Quantum Base Station, and Collar SW software (Version 2.09, Telemetry Solutions).

As soon as possible after the discovery of piping plover nests in areas being used by one or more GPS-collared red foxes, we reprogrammed collars to temporarily increase the frequency of location recording from every 2 hours to every 15 minutes for 2 days before and after predator exclosure setup, egg pipping, and egg hatching at piping plover nests. Due to battery life limitations, we only could sustain this 15-minute location sampling schedule for 8 days per collar while maintaining regular location sampling through the end of the chick-rearing season each August.

In situations where multiple nests were discovered within a given red fox’s territory, we based our programming on the dates corresponding to the first discovered nest. For nests discovered in

areas used by multiple red foxes, we selected foxes based on the proximity of fox core use areas to nest locations. All field methods were approved by Virginia Tech's Institutional Animal Care and Use Committee (Protocol 15-119).

Assessing Spatial Response

We used location data collected from red foxes during the 48-hour periods before and after nest enclosure set-up, first sign of pipping, and hatching to examine spatial responses to these events at 2 spatiotemporal scales. We excluded locations that were not based on enough satellites (>3) to record a high-quality fix. We also excluded locations that fell $>10\text{m}$ into the ocean surrounding the island and those with recorded elevation of $>100\text{m}$ (i.e., well above the highest known point on the island), assuming that such locations were erroneous. We then separated the location data from each 48-hour time period of interest for each red fox and calculated the distance from each red fox location recorded during that time window to the nest of interest using the "spDist" function in R package 'sp' (Version 1.3-1, cran.r-project.org/web/packages/sp, accessed 30 November 2019).

The predicted dates for nest enclosure setup, pre-hatch pipping and hatch at some nests did not coincide with the actual dates, resulting in temporal mismatches between our high frequency data collection and the target events for those events. For all analyses, we used the highest frequency location data available for the 48-hour periods before and after the target event, thus analyses were based on a mix of high frequency (i.e., every 15 min) and regular frequency (i.e., every 1-2 hours) location data. Enclosure setup dates were recorded by management agencies, but not times, so we used 1200 (noon) on the recorded setup date as our cutoff between pre- and post-setup locations. Similarly, the exact pipping and hatch times usually were unknown, although dates were recorded. We used 0600 as the cutoff for pre- vs. post-pipping and 1200 as the cutoff for pre- vs. post- hatching, as we observed that nests typically hatched between 0600 and 1200. Red foxes for whom <10 locations were recorded in one or both (pre- and post-) periods surrounding an event were excluded from that set of statistical comparisons.

We first compared mean distances from locations to nests for all GPS-collared red foxes before vs. after each type of event to determine whether there was evidence of a similar directional response across individuals. We used permutation tests for matched pairs [PTMP], a variation of blocked multiple response permutation procedures [MRBP] that can be used to conduct permutation-based comparisons of paired sample data (McCune and Grace 2002, Cade and Richards 2005). In these analyses, we used the mean distance to nest for each red fox as the response variable, time period (pre- vs. post-event) as the grouping variable, and individual identification as the blocking/pairing variable. We then conducted a series of separate comparisons for each red fox of all recorded distances to the nest before vs. after each type of event using multiple response permutation procedures [MRPP] (McCune and Grace 2002) to further investigate individual-level responses. In these analyses, we used all recorded distances to nest as the response variable and time period (pre- vs. post-event) as the grouping variable. We did not align the data before conducting analyses, as alignment is generally not recommended for paired comparisons (McCune and Grace 2002). We used Blossom Statistical Package (Version W2008.04.02, <https://www.usgs.gov/software/blossom-statistical-package>, accessed 4 June 2020) to conduct these analyses, following the guidelines described by Cade and Richards (2005). While MRPP and PTMP can be used to determine whether data in different groupings (i.e., pre- vs. post-event distances) were more similar than expected by chance, suggesting a statistically significant change, these tests do not indicate the direction of change. Thus, we compared the distribution and/or mean values of the raw data between the two groups to determine whether distances generally increased or decreased. If red foxes were attracted to exclosure setup, pipping, or hatching, we would expect to see a decrease in the mean distance, or a shift in the distribution of distances to shorter distances, from red fox locations to nests after these events. Conversely, if red foxes were not attracted to exclosure setup, pipping, or hatching, we would expect to see no change in the mean distance or distribution of distances from red fox locations to nests after these events.

We then compared the proportion of locations within a 100-m buffer around nests recorded during the 48-hour time periods before vs. after exclosure setup, pipping, and hatching. Estimated GPS location error was $\leq 25\text{m}$ for $>95\%$ of red fox locations that recorded a '3D' fix during our field tests in the open or sparsely vegetated areas of dry sand in which piping plovers nested (Walker et al. 2019, Robinson et al. 2020). Accounting for this $\leq 25\text{-m}$ error, a 100-m buffer should include any locations within 0–75 m of the nest. We used the "spDist" function in R package 'sp' to calculate the distance from each red fox location to the nest of interest. We then used these distances to calculate the proportion of each red fox's locations that fell $<100\text{m}$ from the nest. We compared the proportions of locations in this buffer from each 48-hour period before vs. after each type of event using permutation tests for matched pairs [PTMP] as described above, and compared the data distributions to determine the direction of any observed responses. If red foxes keyed in on exclosure setup, pipping, or hatching, we would expect to see an increase in the proportion of locations within the buffer area after these events. Conversely, if red foxes did not key in on exclosure setup, pipping, or hatching, we would expect to see no change in the proportion of locations within the buffer area after these events.

Results

Red Fox Trapping, GPS Collaring, and Tracking

We captured, GPS-collared, and reprogrammed GPS collars to the high frequency sampling schedule for 5 red foxes in 2016 and 5 red foxes in 2017 whose home ranges overlapped with plover nesting areas. The number of locations recorded for each red fox during the 48-hour periods before and after exclosure setup, pipping, and hatching varied considerably (Table 42). One red fox was captured, collared, and monitored during both the 2016 and 2017 monitoring period, resulting in 2 location datasets from that fox. We treated these datasets as independent, given the difference in breeding season and geographic shift in that fox's territory between breeding seasons ($\sim 500\text{m}$ westward between 2016 and 2017 breeding seasons), for a total of 10 location datasets collected.

Table 42. Number of GPS locations recorded for each red fox during each 48-hr period of interest on Fire Island, NY in 2016-2017. Foxes for whom <10 locations were recorded in one or both (pre- and post-) periods surrounding an event were excluded from that set of statistical comparisons.

Year	Fox	Nest ID ^b	Exclosure		Pipping		Hatching	
			Pre	Post	Pre	Post	Pre	Post
2016	F-05	211	85	126	165	8	10	13
2016	F-07	204	53	140	107	186	185	125
2016	F-09	32	93	183	12	10	11	12
2016	F-10	32	105	184	12	9	12	11
2016	M-08 ^a	211	75	118	159	10	10	17
2017	F-11	203	149	24	184	155	8	11
2017	F-12	205	175	64	158	166	9	10
2017	F-13	211 ^c	190	54				
2017	M-08 ^a	214	6	128	20	0 ^d	0 ^d	0 ^d
2017	M-17	211 ^c	183	52				

^aThis fox was captured and monitored during both 2016 and 2017; the 2 location datasets were treated as independent in analyses

^bUnique nest identifier used in field monitoring and data management steps (C.C. Robertson et al., Virginia Tech, unpublished report)

^cNest failed in between exclosure setup and estimated hatch date

^dCollar malfunction resulted in no usable data during these periods

Assessing Spatial Response

Mean distances from red fox locations within individual home ranges to nests were similar before vs. after exclosure setup (Mean distance to nest across individuals $\bar{x}$ = 641m before, 675m after; PTMP, T = 0.28, P = 0.56, n = 9 foxes), but decreased following the first sign of pipping at nests ($\bar{x}$ = 550m before, 507m after; PTMP, T = 0.00, P ≤ 0.001, n = 5 foxes) and increased following hatching ($\bar{x}$ = 773m before, 794m after; PTMP, T = 0.00, P ≤ 0.001, n = 5 foxes; Table 43, Figure 45).

Despite the lack of a population-level change in mean distances to nest following exclosure setup, our individual-level MRPP comparisons identified shifts in distances to nest for 4 of the 9 red foxes included in our analyses, with 2 red foxes using locations that were on average closer to nests (Fox F-07: MRPP, $T = -2.39$, $P = 0.04$, $n = 193$ locations; Fox F-13: $T = -2.56$, $P = 0.03$, $n = 244$ locations, respectively) following setup and 2 red foxes using locations that were on average further from nests (Fox M-17: MRPP, $T = -9.04$, $P \leq 0.001$, $n = 235$ locations; Fox F-05: $T = -10.26$, $P \leq 0.001$, $n = 211$ locations) following setup (Table 43). We observed similar variation among individuals in our MRPP comparisons surrounding pipping, with 2 of 5 red foxes using locations that were on average closer to nests (Fox F-07: MRPP, $T = -23.84.42$, $P \leq 0.001$, $n = 293$ locations; Fox F-12: $T = -10.84$, $P \leq 0.001$, $n = 234$ locations) and 1 red fox using locations that were on average further from nests (Fox F-11: MRPP, $T = -9.42$, $P \leq 0.001$, $n = 339$ locations) following pipping (Table 43). None of the 5 red foxes included in our hatching comparisons showed significant differences in distances from their locations to nests before vs. after hatching.

The proportions of red fox locations within 100-m buffers surrounding nests were generally low (mean proportion across all foxes < 0.13 for all pre- and post-event periods) and did not differ before vs. after exclosure setup (PTMP, $T = 0.26$, $P = 0.53$, $n = 9$ foxes), pipping (PTMP, $T = -1.00$, $P = 0.16$, $n = 5$ foxes), or hatching (PTMP, $T = 0.65$, $P = 0.73$, $n = 5$ foxes; Table 44, Figure 46).

Table 43. Mean distances from GPS-collared red fox locations to piping plover nests in a red fox's home range on Fire Island, New York for each red fox and 48-hr period of interest in 2016–2017, and differences in mean distances (Δ) following events, in meters. Percent change is shown (% Δ), and represents $((\text{Post}-\text{Pre})/\text{Pre}) \times 100$. The mean distances, differences, and percent change across all foxes are also shown. Foxes for whom <10 locations were recorded in one or both (pre- and post-) periods surrounding an event were excluded from those statistical comparisons, and are not included in this table.

Year	Fox ^a	Nest ^b	Exclosure				Pipping				Hatching			
			Mean or Δ Distance (m)				Mean or Δ Distance (m)				Mean or Δ Distance (m)			
			Pre	Post	Δ	% Δ	Pre	Post	Δ	% Δ	Pre	Post	Δ	% Δ
2016	F-05	211	451	627	175	38.8 [^]					347	422	75	21.5
2016	F-07	204	408	398	-10	-2.4 [^]	275	187	-88	-32.1 [^]	202	200	-2	-0.9
2016	F-09	32	1131	1167	36	3.2	1151	1210	59	5.2	1204	1203	-1	-0.1
2016	F-10	32	1354	1369	14	1.1					1825	1827	2	0.1
2016	M-08	211	481	476	-5	-1.1	459	303	-156	-34.0	286	318	32	11.1
2017	F-11	203	239	240	1	0.2	289	294	5	1.7 [^]				
2017	F-12	205	586	542	-44	-7.5	575	541	-34	-6.0 [^]				
2017	F-13	211 ^c	638	576	-62	-9.8 [^]								

2017	M-17	211 ^c	477	677	200	41.9 [^]								
	Mean		641	675	34	7.2	550	507	-43	-13.0*	773	794	21	6.3*

^a M denotes males, F denotes females

^b Unique nest identifier used in field monitoring and data management steps (C.C. Robertson et al., Virginia Tech, unpublished report)

^c Nest failed in between exclosure setup and estimated hatch date

* denotes $P \leq 0.05$ in overall permutation test for matched pairs [PMTP] comparison

[^] denotes $P \leq 0.05$ in individual multiple response permutation procedure for matched pairs [PMTP] comparison

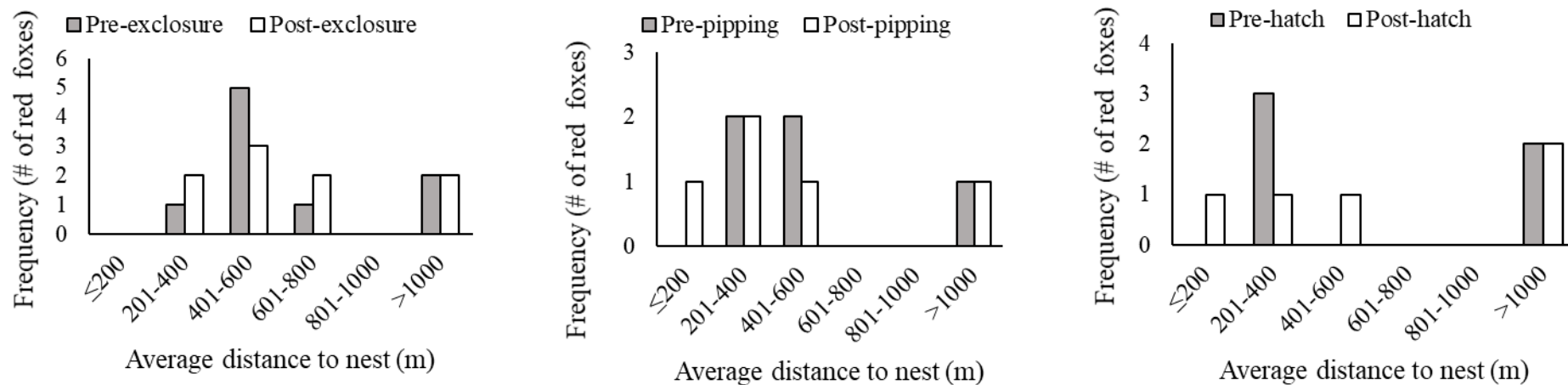


Figure 45. Distribution of average distances from GPS-collared red fox locations to piping plover nests during 48-hr periods before vs. after exclosure setup (left, n=9), pipping (middle, n=5), and hatching (right, n=5) on Fire Island, New York in 2016-2017.

Table 44. Proportion of GPS-collared red fox locations within a 100-m buffer surrounding piping plover nests on Fire Island, New York for each red fox and 48-hr period of interest in 2016–2017. Change in proportion (Δ) is shown, and represents (Post-Pre). The mean proportions and changes across all foxes are also shown. Foxes for whom <10 locations were recorded in one or both (pre- and post-) periods surrounding an event were excluded from those statistical comparisons, and are not included in this table.

Year	Fox ^a	Nest ^b	Exclosure			Pipping			Hatching		
			Proportion or Δ Proportion of points $\leq$ 100 m of nest			Proportion or Δ Proportion of points $\leq$ 100 m of nest			Proportion or Δ Proportion of points $\leq$ 100 m of nest		
			Pre	Post	Δ	Pre	Post	Δ	Pre	Post	Δ
2016	F-05	211	0.01	0.00	-0.01				0.20	0.00	-0.20
2016	F-07	204	0.00	0.00	0.00	0.13	0.46	0.33	0.37	0.45	0.08
2016	F-09	32	0.00	0.01	0.01	0.00	0.00	0.00	0.00	0.08	0.08
2016	F-10	32	0.00	0.00	0.00				0.00	0.00	0.00
2016	M-08	211	0.00	0.10	0.10	0.01	0.10	0.09	0.10	0.06	-0.04
2017	F-11	203	0.01	0.08	0.07	0.01	0.03	0.03			
2017	F-12	205	0.01	0.00	-0.01	0.02	0.02	0.00			
2017	F-13 ^c	211	0.02	0.04	0.02						
2017	M-17 ^c	211	0.06	0.00	-0.06						
Mean			0.01	0.03	0.01	0.03	0.12	0.09	0.13	0.12	-0.02

^a M denotes males, F denotes females

^b Unique nest identifier used in field monitoring and data management steps (C.C. Robertson et al., Virginia Tech, unpublished report)

^c Nest failed in between exclosure setup and estimated hatch date

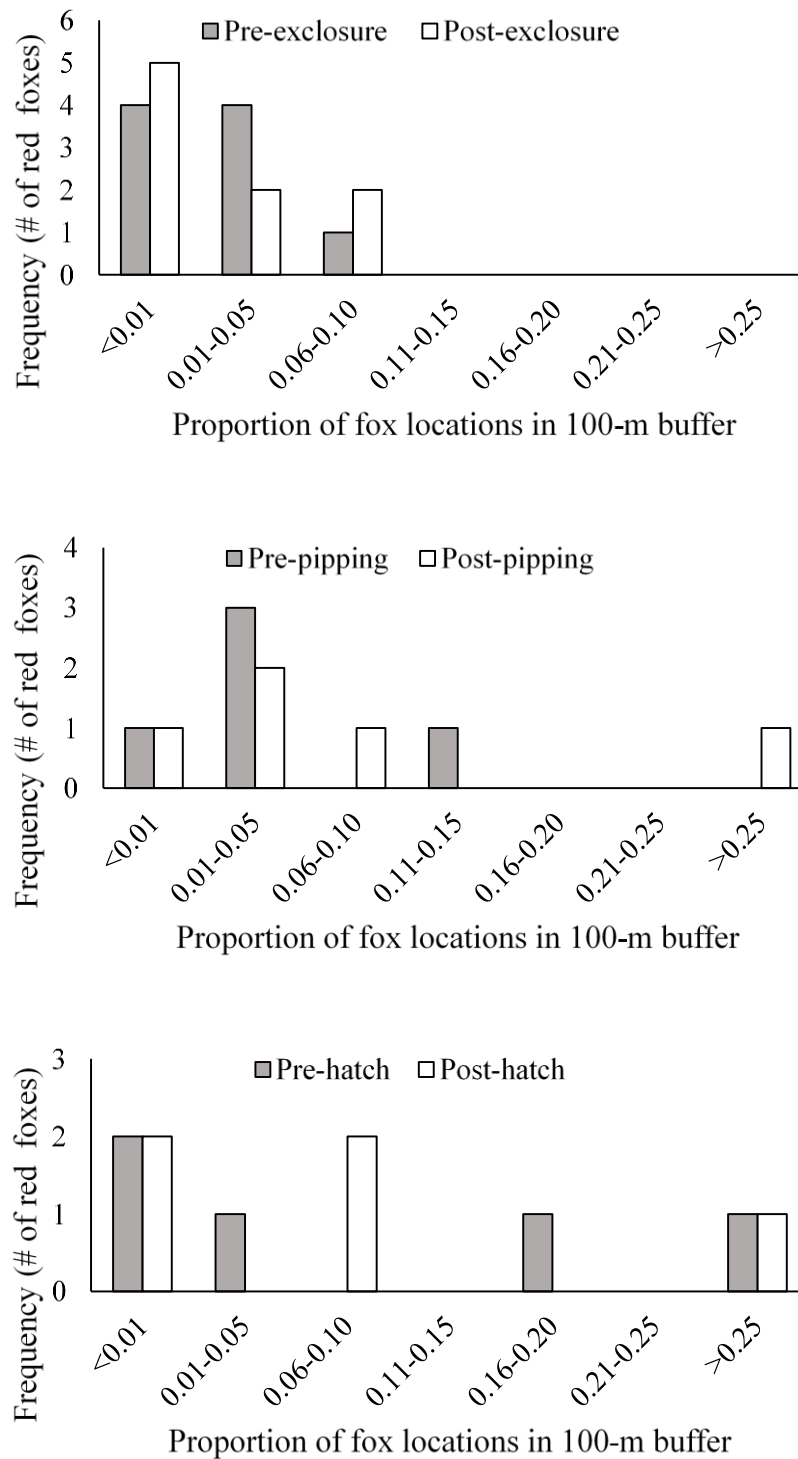


Figure 46. Distribution of the proportions of GPS-collared red fox locations within 100-m buffers surrounding piping plover nests during 48-hr periods before vs. after exclosure setup (top, n=9), pipping (middle, n=5), and hatching (bottom, n=5) on Fire Island, New York in 2016-2017.

Discussion

To our knowledge, this is the first study that has attempted to use GPS location data to examine spatial responses of predators to nest exclosures or hatching. Previous studies have used GPS location data to examine spatial overlap between predators and prey nest locations, general nesting areas, and other spatially predictable prey sources. For example, Fiderer et al. (2019) used GPS location data from red foxes and raccoons (*Procyon lotor*) to examine predator habitat selection and movement patterns relative to ground-nesting bird distribution in Brandenburg, Germany. Based on these habitat and space use patterns, they inferred likely differences in predation pressure among different groups of ground-nesting birds between the two predator species. Similarly, Lei and Booth (2018) used GPS location data from yellow-spotted goannas (*Varanus panoptes*) and lace monitors (*Varanus varius*) to describe spatial overlap between the two monitor lizard species and loggerhead sea turtle (*Caretta caretta*) nests in southeast Queensland, Australia. Roth and Lima (2007) used GPS location data to determine whether sharp-shinned hawks (*Accipiter striatus*) in Indiana focused their hunting activities near birdfeeders. In addition, Votier et al. (2010) used a combination of GPS, stable isotope, and vessel monitoring systems data to examine the foraging behavior of breeding northern gannets (*Morus bassanus*) relative to fishing trawlers and the associated scavenging opportunities.

In our study using GPS collars to track predator responses to nest exclosures, hatching and pipping, red foxes did not exhibit a consistent spatial response to exclosure setup, and exhibited mixed responses to piping plover pipping and hatching. Specifically, the observed decrease in mean distance from red fox locations to nests within their home ranges in the 48-hr period following pipping is consistent with the idea that red foxes may be attracted to nests by the beginning of the pre-hatch pipping process. However, the mean distance of red fox locations to nests post-pipping was still > 500m. The observed increase in mean distance from red fox locations to nests in the 48-hr period following hatching suggests that any potential attraction during pipping may dissipate as chicks emerge from eggs and leave the immediate area of the nest.

We did not find any evidence of a relationship between red fox space use in the immediate vicinity of nests and the setup of exclosures, pipping, or hatching at these nests during this study. However, signs of red fox digging and circling at exclosures were observed at Smith Point County Park during the 2015 and 2018 piping plover breeding seasons (C.C. Robertson et al., Virginia Tech, unpublished report), suggesting that red fox responses to nest exclosures may vary from year to year. It is also possible that red foxes in our study approached exclosures during any or all of our events, but the approaches were brief enough to not be captured in any of the 15-min, 1-hr or 2-hr location fixes. In other analyses of GPS-collared red fox movements in the study area, Black et al. (*Chapter 3*/K.M. Black, Virginia Tech, unpublished data) estimated a mean hourly movement rate of 216.3 m/hr $\pm$ 8.7 m/hr (SE) across all hours, and a mean hourly movement rate of 366.5 m/hr $\pm$ 14.8 m/hr (SE) during nighttime periods when foxes were most active. Thus, it is possible that a GPS-collared red fox could have approached a nest and then left the vicinity in between location fixes.

Our findings differ from those of Beaulieu et al. (2014), who used remote cameras to observe predator visits at nests and found that red foxes linger outside of exclosed nests for longer and visited exclosed nests more often compared to unexclosed nests. These differences in conclusions may be due to methodological differences between the 2 studies. While cameras may be better-suited to recording repeated brief red fox visits to nests than the 15-min to 2-hr location data that we used, cameras do not record instances in which red foxes did not visit a nest within their territory. We recommend that future investigations into red fox behavior at plover nests take advantage of both data collection approaches. Concurrent remote camera monitoring of some plover nests within the study area documented regular red fox visitation at exclosed nests, but none of the foxes in these nest camera photographs appeared to have GPS collars (C.C. Robertson et al., Virginia Tech, unpublished report; C.C. Robertson, Virginia Tech, unpublished data). Because not all nests included in this study were monitored by cameras, it is also possible that GPS-collared foxes could have visited an exclosure but were not photographed doing so. These differences may also be due to the differences in experimental design. While most previous studies examining predator responses to exclosures have

compared detections at exclosed vs. unexclosed nests, we did not find any other studies that compared detections at the same nest before vs. after exclosure setup.

In the absence of clear evidence that red foxes are drawn to nest exclosures, we recommend continued exclosure use within our study area, as whether or not a nest was exclosed was the strongest predictor of piping plover nest survival during the study (C.C. Roberston, Virginia Tech, unpublished report). However, we also recommend that managers continually re-evaluate the effects of nest exclosures at their sites, as changes in background nest predation rates, abandonment rates, and plover adult survival may all influence the relative benefit of nest exclosures for population growth rates (Cohen et al. 2016). Darrah et al. (2020) present a decision support tool that managers can use to determine whether or not to use exclosures, given site-specific nest fate information. In addition, future studies could compare movements of GPS-collared red foxes to movements of marked piping plover chicks to further quantify spatial relationships between shorebirds and their predators.

Section 4: Dietary ecology of red foxes

This section describes data collection, analytical methods, and results related to the following objectives for red fox monitoring associated with the Fire Island Inlet to Moriches Inlet Fire Island Stabilization Project during the 2015-2020 monitoring period. We were not able to collect additional field data in 2020 due to covid-19 restrictions.

Objective 5: Quantify the interactions of red foxes with shorebird nests and chicks.

In Part 3, Section 3 of this report, we also describe the spatial interactions of red fox and piping plovers as part of this objective. We opted to break out the monitoring results on diet into this separate report section given the very different nature of the two types of data related to this monitoring objective.

Introduction

The dietary ecology of red foxes (*Vulpes vulpes*) has been studied extensively, spanning a variety of geographic locations and ecosystems (see Lloyd 1980, Ables 1983, Henry 1986, Soulsbury et al. 2010, and others for summaries). In general, red foxes are opportunistic omnivores that will eat a wide range of items including fruit and plant matter, insects, rodents, lagomorphs, small birds, fish, and other freshwater or marine organisms when available, and will also scavenge upon carcasses of larger animals. Relative availability and ease of attainment influence the proportions of red fox diets comprised of specific items (Ables 1983, Lloyd 1980).

Despite the wealth of information on red fox diets in the existing literature, there is relatively little information on red fox diets in North American coastal ecosystems, particularly on the U.S. Atlantic coast and on barrier islands. Previous research suggests that small mammals and birds comprise a significant portion of red fox diets in these systems. In a study of coastal red fox diets on Assateague Island, MD, Krim et al. (1990) reported rabbit, vole, mouse, and other mammal remains occurring most frequently in collected scats (87% of samples), with evidence of frequent crustacean (64.8%) and bird (46.3%) consumption as well. On Fire Island, NY, Peterson et al. (2020) found remains

of birds and cricetid rodents most frequently in scat samples, occurring in 39% and 37.8% of samples, respectively.

Red fox diets in developed coastal areas may be influenced by anthropogenic food availability. Anthropogenic foods may include scavenged or intentionally fed scraps, food left out for pets, produce from gardens and compost heaps, and waste material from unsecured trash containers; these foods have been shown to be the most common items in red fox diets in some developed areas (Soulsbury et al. 2010). Where fishing occurs, discarded bycatch also may be available, allowing red foxes to access aquatic food sources more easily. For example, Krim et al. (1990) frequently observed skate (Family Rajidae) and bluefish (*Pomatomus saltatrix*) remains outside of red fox dens on Assateague Island and hypothesized that they were scavenged from angler discards. Access to anthropogenic food sources has been shown to increase the abundance of red foxes and other mesopredators, leading to increased predation on prey and even potentially altering prey behavior (Shapira et al. 2008, Newsome et al. 2015). This increase in predation can be particularly problematic when threatened and endangered species are affected (Gompper and Vanak 2008).

Red foxes are known to depredate federally threatened piping plover (*Charadrius melodus*) nests at many sites in their Atlantic coast breeding range (Rimmer and Deblinger 1990, Patterson et al. 1991, Melvin et al. 1992, Cohen et al. 2010). As a result, extensive lethal and nonlethal red fox control efforts are conducted in piping plover nesting areas along the U.S. Atlantic coast (Hunt et al. 2019a). However, it is unknown whether plovers and other shorebirds make up a large proportion of red fox diets in these areas. Although Krim et al. (1990) found bird remains in 46.3% of scat samples collected in May–August on Assateague Island, when piping plovers and other shorebirds nest on the island, the authors did not report a taxonomic breakdown of identified bird remains. Peterson et al. (2020) did not observe any piping plover remains in red fox scats collected along boardwalks on Fire Island in 2011–2012, but the island’s piping plover population has increased substantially since the years of their scat collection (Walker et al. 2019, Weithman et al. 2019, Robinson 2020), likely increasing relative availability of this species across the landscape. As many piping plover breeding areas along

the Atlantic coast experience heavy seasonal human use, it is important to consider whether anthropogenic food resources might be subsidizing populations of red foxes and other predators in these settings. If so, these anthropogenic food resources could be indirectly influencing predation pressure on piping plovers and should be considered in management planning.

The goals of this monitoring were to investigate red fox dietary ecology on Fire Island, New York in light of increasing piping plover numbers and to explore the effects of anthropogenic food resources on the island's fox population. We also sought to expand upon the work conducted by Peterson et al. (2020) by characterizing red fox diets on the island using scats collected across additional habitat types and geographic areas. We used fecal dietary analyses to identify major prey species and compare dietary composition relative to piping plover breeding and tourist seasons. We also conducted den prey item surveys to provide a secondary index of red fox dietary composition on the island. Finally, we examined the relationships among anthropogenic food waste at dens, proximity to development, and litter size to determine whether anthropogenic resources might be subsidizing the island's red fox population via increased reproduction. If so, we would expect there to be a positive correlation between human food waste and/or fish remains recorded at dens and estimated litter sizes.

Methods

Field methods

We conducted repeated transect surveys to locate potential red fox scats and breeding dens. We used ArcMap 10.3 GIS software (ESRI 2014) to create and overlay a 300-m x 300-m grid on each of the 3 focal study areas. Using this grid overlay, we established 96 walking transects from the ocean beach high tide line to the bayside high tide line, or the point where bayside habitat became impassible due to dense vegetation or deep marsh. Transects generally passed over the center points of the grid cells across the island, such that each transect was ~300 m from the next. This 300-m grid size was initially selected because Gieder (2015) found that red foxes on Assateague Island, MD,

moved infrequently between camera stations spaced ~300m apart. Home range estimates based on concurrent GPS monitoring suggest that this spacing was sufficient to ensure that each red fox home range encompassed ≥ 2 transects. Our transects ran perpendicular to the general west-east linear distribution of different habitats on the island and spanned all passable habitat types found within each 300-m section covered by each transect (Figure 29). The exact route followed on each transect during a given survey was determined based on observed tracks and signs, to maximize the likelihood of locating scats and other features of interest. Following game trails, edges, and other likely wildlife travelways, we walked each transect across the island approximately once per month during the red fox denning and piping plover breeding seasons (May, June, July) and again outside of the breeding seasons in October/November, December, and January/February of 2016–2019, ending in February 2019.

During these surveys, we searched for potential red fox scats and collected all scats that appeared to be ≤ 1 -month old (based on color, moisture, and biodegradation; Table 45). Additional fresh scat samples were collected opportunistically throughout the year during concurrent monitoring activities in the study area, including den monitoring visits, trapping, and shorebird surveys. We also searched for and recorded potential active red fox den sites. In 2017 and 2018, we conducted additional transect surveys in late April/early May to locate active red fox breeding dens. During these surveys, multiple observers worked together to search all accessible areas for potential dens, in addition to the game trails and transect areas typically surveyed during other months. Potential dens also were located opportunistically during concurrent monitoring activities in the study area, including GPS-collaring and ear-tagging and tracking of adult red foxes in the study area (Part 3, Section 1). We revisited all potentially active dens within 2 weeks of discovery to re-assess their status. Dens that still appeared active during this second visit were monitored every 2 weeks until they were no longer active, as determined by 2 visits with no new signs of red fox use, including tracks in and out of the den, fresh scats, new prey items, and red foxes seen in the vicinity.

Table 45. Scat collection criteria used in sign, scat, and den surveys conducted on Fire Island, New York in 2016–2019. “Fecal material” refers to the unidentifiable digested waste material contained in a sample, as opposed to the identifiable prey item remains.

Age Category	Color	Moisture	Biodegradation	Notes
Very fresh (<24 hours old)	Varied	Very moist	None	Observed a fox depositing the sample and/or fresh fox sign within 2m. Collect.
Fresh (24 hours-a few days old)	Usually dark	Somewhat moist	None	Collect
Mid (≥ a few days old)	Usually somewhat dark, no sun bleaching	May be moist due to recent dew/humidity	None, outer fecal material intact	Collect. Sample photo: 
Old (≤1 month old)	Usually lighter, may be sun bleached	Usually dry	Some, outer fecal material beginning to wear away but still present	Collect only if outer fecal material is mostly intact. Sample photo: 
Very Old (> 1 month old)	Usually very light, sun bleached	Very dry	Significant, hardly any outer fecal material left	Do not collect

During den monitoring visits, we collected scats and recorded and photographed prey remains in a ~15 m radius around the den. Adult red foxes commonly bring prey items back to the den to provision their young; this radius encompassed the area where prey items were left. We also recorded any adult red foxes or kits in the area. To assist in determining the number of kits associated with each den, we set up one or more remote cameras (Moultrie M880i, EBSCO Industries, Calera, AL) aimed at den entrances and/or adjacent clearings, when feasible. We did not use remote cameras at dens in areas of high human use to avoid drawing attention to dens. Where cameras were used, we changed memory cards and batteries and adjusted camera orientation during den monitoring visits. Most red fox family groups used multiple breeding dens throughout the breeding season. To account for these relocations in later analyses, we used remote camera photos and in-person observations of kits, and information on family group movements based on GPS-collared and ear-tagged red foxes, to classify dens as either natal dens (used early in denning season and in weeks following parturition, typically active through late May) or secondary dens (used later in the season, created or re-excavated after kits had emerged from dens, typically active starting in late May/early June).

Upon collection in the field, scat samples were stored in individually-labeled paper bags. At the end of each day, these collected samples (still in their paper bags) were placed in individually-labeled Ziploc bags and frozen to 0° C. At the end of each field season, we transported all collected samples on ice back to Virginia Tech and stored them at -20° C until analysis. All field methods were approved by Virginia Tech's Institutional Animal Care and Use Committee (Protocol 15-119), and followed the American Society of Mammalogists' guidelines for research on wild animals (Sikes et al. 2016).

Genetic analyses

Analyses based on incorrect field identification of source species can lead to biased descriptions of dietary composition (Morin et al. 2016). Given the presence of other mesopredators on the island and the similarity in morphology between red fox scats and non-target species scats, we genetically verified the source species of samples collected. Prior to conducting diet analyses, we

separated a small portion (approximately 2ml) of fecal material from the outside edges and tapered ends of each scat sample, and submerged this portion in 95% ethanol for DNA preservation. These preserved subsamples were sent to the Mammalian Ecology and Conservation Unit (MECU) in the Veterinary Genetics Lab at University of California, Davis for mitochondrial DNA sequencing to verify the source species (Aubry et al. 2009, Miles et al. 2015). For a subset of scat samples shown to contain high-quality red fox DNA, we examined 22 nuclear DNA microsatellite loci and attempted to distinguish among samples originating from different red foxes using individual genotypes (Sacks et al. 2010, 2011; Quinn et al. 2019).

Fecal dietary analyses

Following DNA subsampling, we used the remaining portion of each scat sample for fecal dietary analysis. We freeze-dried samples for ≥ 48 hours to remove any remaining moisture, then separated out and sorted contents by hand. We identified contents to the lowest taxonomic level possible through comparison to a variety of resources, including field guides, online and/or published reference materials (including Spiers 1973, Debelica and Thies 2009), and museum specimens. We used a dissecting microscope to assist with identification of scat contents as needed, and we used a digital compound light microscope to assist with identification of hair and feathers. We visually separated hairs and feathers into groups based on morphological similarity and examined 3-6 representative samples from each group. For hairs, we examined the internal medulla and external cuticular scales, selecting both guard hairs and underfur when present (Debelica and Thies 2009). We then compared these hairs to a hair microscopy guide for 23 mammal species found in our study area, created using hairs from known identity specimens in the Virginia Tech Department of Fish and Wildlife Conservation's Natural History Museum (Table 46), and other pre-existing hair microscopy guides (Spiers 1973, Debelica and Thies 2009). For feathers, we focused our examinations on the barbs and barbules of plumulaceous feathers, as those sections contain the most useful diagnostic characteristics (Dove and Koch 2010).

Table 46. Link to hair microscopy guide created using hairs from museum specimens in the Virginia Tech Department of Fish and Wildlife Conservation's Cheatham Hall Natural History Museum. We used this guide to assist in identifying hairs found in fecal samples collected opportunistically, during systematic surveys, and at dens sites on Fire Island, New York in 2016–2019.
<https://zookat13.wixsite.com/research/resources>

Overall and seasonal frequency of occurrence in scats

We calculated frequency of occurrence for each diet item found in red fox scats, defined as the proportion of all scat samples containing at least one item in a given category (Klare et al. 2011, Larson et al. 2015). While many different indices can be used to describe dietary composition, frequency of occurrence indices are most commonly reported for carnivore fecal dietary analyses (Klare et al. 2011), allowing our results to be comparable to many other studies. We calculated frequency of occurrence by scat sample at the broad categorical level (anthropogenic, bird, fish, shellfish, insect/arachnid, mammal, reptile, vegetation, and unknown [any item not clearly identifiable as belonging to another category]), then by order and species when possible. Items that were not identifiable to species were labeled to the lowest identifiable taxonomic level, i.e., "Order Rodentia." We excluded red fox hair found in samples from our analyses, as it was likely ingested during grooming. We also excluded miscellaneous natural non-food items found in scats, such as rocks and beach debris, that were likely either ingested unintentionally by red foxes while eating other items, or unintentionally collected by researchers in sample bags during the scat collection process.

Seasonal diet comparisons from scat samples

To determine whether red fox dietary composition varied seasonally, we separated scat samples into one of two seasonal categories based on the month in which they were collected: "Fall/Winter" for samples collected in September–March, and "Spring/Summer" for samples collected in April–August. The Spring/Summer collection period aligned with the piping plover breeding season

on the island, and encompassed most of the tourist season, which unofficially runs from Memorial Day to Labor Day, and fox denning season on the island. We compared the frequency of occurrence for each broad category of food item between samples collected in Fall/Winter vs. Spring/Summer, using separate Pearson's chi-square tests for equal proportions and excluding any categories in which prey items were not found in at least one sample in each season, with the null hypothesis that proportions for each category would be equivalent between seasons ($\alpha=0.05$, Wright 2010).

Individual diet comparisons

To explore whether individual red foxes might be specializing on certain types of prey, we compared the contents of different scat samples that came from the same individual red foxes, based on microsatellite genotyping results. Using information from all individuals for whom >3 scat samples were collected, we calculated the average number of categories, orders, and species consumed per individual.

Den prey item analyses

We estimated frequency of occurrence by den for prey remains and food items recorded within the 15-m radius of active red fox dens, defined as the proportion of dens with at least one item belonging to a given category. We also calculated frequency of occurrence by item at dens, or the proportion of all items belonging to a given category, collected across all dens (Klare et al. 2011, described as percent occurrence by Larson et al. 2015). In this case, frequency of occurrence by den reflects how often a given item is consumed by a red fox breeding group at a den, while frequency of occurrence by item reflects the proportion of the total diet of red fox breeding groups at a den made up by that item.

Proximity to development, anthropogenic food waste at dens, and red fox litter sizes

To determine whether anthropogenic food waste might be subsidizing the red fox population, we compared relative amounts of anthropogenic food found at breeding dens, proximity of breeding dens to development, and estimated litter sizes. To calculate distances to development for each den, we used ArcMap 10.6 (ESRI 2018) and annual aerial imagery (flown 2015–2018) to delineate all developed areas on the island, including residential areas, visitor centers, paved roads, parking lots, and boardwalks. We then used the “Euclidean Distance” tool in ArcMap to create a 1m resolution raster layer containing the distances from each pixel to the nearest pixel of developed habitat. Finally, we overlaid the locations of all breeding dens (natal and secondary), onto this raster layer and used the “Extract Multi Values to Points” tool to extract the distance to development values for each den location.

To account for multiple potential sources of anthropogenic food subsidies and differing monitoring periods among dens, we included the daily rates of accumulation (# items found/total days monitored) of both human food waste and fish remains in our comparisons. We used records of kits observed during den monitoring visits and photographed on remote cameras to estimate litter sizes for each den. Because kits were not uniquely identifiable, we conservatively used the maximum number of kits recorded in a given photo or den monitoring visit during the time in which that den was active. Thus, these numbers represent a minimum estimate of the number of kits that emerged from each den.

We conducted separate comparisons using information from natal vs. secondary dens. As not all dens had prey items in the vicinity, we limited our comparisons involving human food waste and fish remains to only those dens where prey remains of any type were recorded. We calculated Spearman’s rank correlation coefficient (Spearman 1904) for each of the following comparisons to test whether any of these factors were correlated: distance to development vs. human food accumulation rates, distance to development vs. fish remain accumulation rates, distance to development vs. litter size, human food accumulation rates vs. litter size, and fish remains accumulation rates vs. litter size.

Results

We collected 300 potential red fox scat samples opportunistically (n = 21), during transect surveys (n = 223), and during den monitoring (n = 56). We collected DNA subsamples from 267 of these scat samples for genetic verification of source species. The remaining 33 samples were not suitable for genetic analyses due to age, biodegradation, or damage sustained during field transport. Of the samples analyzed, 220 of 267 yielded a source species identification, resulting in a genetic species identification success rate of 82.4%. Of these samples, 96.8% (213 out of 220 samples) were identified as red fox. Of the seven non-fox scat samples, two were identified as white-tailed deer (*Odocoileus virginianus*, presumed to be DNA from prey), two were identified as domestic dog, and three were identified as domestic cat. Given the high genetic source species verification rate of potential red fox samples examined, we included the 33 samples that were not sent for source species verification and the 47 samples that failed to yield a source species identification during genetic analyses in our red fox dietary analyses, for a total of 293 confirmed (n = 213) or probable (n = 80) red fox samples.

Fecal dietary analyses

Red foxes on Fire Island, NY in 2016–2019 had a highly varied diet. Mammal (78% of samples), vegetation (76%), and insect/arachnid (57%) remains were found most frequently in the scats examined (Table 1). We identified 27 taxonomic orders of prey items, of which Rodentia (rodents, 43% of samples), Coleoptera (beetles, 38%), and Decapoda (crabs and other crustaceans, 29%) were the most frequently found (Table 47). Unidentified vegetation (65% of samples), unidentified mammals (28%), and Order Decapoda (27%) were the most frequent lowest identifiable taxonomic levels of items in red fox scats (Table 47). Unidentified vegetation included partially and fully digested remains of various plant species that were not identifiable beyond 'vegetation'. Unidentified mammals consisted primarily of hair and mammal bone fragments that we could not further identify. Order Decapoda included shell fragments from unknown crustacean species, most likely crabs. Of items in

scat that could be confidently identified to the species level, white-tailed deer were the most frequently occurring (12% of samples), followed by the American dog tick (*Dermacentor variabilis*, 11%), and eastern cottontail rabbit (*Sylvilagus floridanus*, 8%).

Table 47. Frequency of occurrence by scat sample, defined as the proportion of scat samples that contained at least one item in a given category, for all prey remains and food items found in fecal dietary analysis of confirmed and probable red fox scat samples (n=293) collected on Fire Island, New York opportunistically, during systematic transects, and during den monitoring in 2016–2019. Results are presented by general category, taxonomic order, and species/lowest identifiable taxonomic level (for items that were not identifiable to species).

Item classification	Frequency of occurrence by scat sample		
	Category	Order	Species/lowest identifiable level
Anthropogenic	0.16	0.16	0.16
Bird	0.35		
Order Anseriformes		0.06	
Family Anatidae			0.05
Unidentified Anseriformes			0.01
Order Charadriiformes		0.03	
Family Charadriidae			0.01
Family Laridae			0.01
<i>Larus spp.</i>			0.02
Unidentified			
Charadriiformes			<0.01
Order Columbiformes		<0.01	<0.01
Order Falconiformes		0.01	
Family Accipitridae			<0.01
Unidentified Falconiformes			<0.01
Order Galliformes		0.01	

<i>Colinus virginianus</i>		<0.01
Unidentified Galliformes		0.01
Order Gruiformes	0.01	0.01
Order Passeriformes	0.06	
Family Parulidae		<0.01
Unidentified Passeriformes		0.06
Unidentified bird, Class		
Aves	0.24	0.24
Fish	0.12	
Unidentified fish	0.12	0.12
Insects and Arachnids	0.57	
Order Araneae	<0.01	
<i>Dysdera crocata</i>		<0.01
Order Coleoptera	0.38	
Family Histeridae		<0.01
<i>Acritus spp.</i>		<0.01
Family Carabidae		0.03
<i>Calasoma scrutator</i>		<0.01
<i>Pterostichus spp.</i>		<0.01
Family Coccinellidae		
<i>Epilachna borealis</i>		<0.01
Family Curculionidae		<0.01
<i>Dendroctonus spp.</i>		<0.01
Family Elateridae		<0.01
<i>Melanotus spp.</i>		0.01
Family Lucanidae		0.01

Family Scarabaeidae		0.04
<i>Phyllophaga spp.</i>		0.11
Unidentified Coleoptera		0.23
Order Hymenoptera	0.01	
Family Formicidae		<0.01
Unidentified Hymenoptera		0.01
Order Ixodida	0.13	
Family Ixodidae		0.01
<i>Amblyomma americanum</i>		0.01
<i>Dermacentor spp.</i>		<0.01
<i>Dermacentor variabilis</i>		0.11
<i>Ixodes scapularis</i>		0.01
Order Odonata	<0.01	<0.01
Order Orthoptera	<0.01	<0.01
Unidentified insect, Class Insecta	0.16	0.16
Unidentified insect/arachnid, class		
unknown	0.01	0.01
Mammal	0.78	
Order Artiodactyla	0.12	
<i>Odocoileus virginianus</i>		0.12
Order Carnivora	0.12	
<i>Felis cattus</i>		<0.01
<i>Procyon lotor</i>		0.07
Family Mustelidae		<0.01
<i>Mustela frenata</i>		<0.01
<i>Mustela vison</i>		0.01

<i>Mustela spp.</i>		0.02
Unidentified Carnivora		0.01
Order Chiroptera	0.02	0.02
Order Didelphimorphia	0.02	
<i>Didelphis virginiana</i>		0.02
Order Eulipotyphla	0.04	
<i>Scalopus aquaticus</i>		0.01
Family Soricidae		0.01
<i>Blarina brevicauda</i>		0.01
<i>Blarina spp.</i>		<0.01
<i>Sorex cinereus</i>		0.01
Order Lagomorpha	0.08	
<i>Sylvilagus floridanus</i>		0.08
Order Rodentia	0.43	
Family Cricetidae		0.01
<i>Microtus pennsylvanicus</i>		0.04
<i>Microtus spp.</i>		0.09
<i>Ondatra zibethicus</i>		0.04
<i>Peromyscus leucopus</i>		0.02
<i>Peromyscus maniculatus</i>		0.01
<i>Peromyscus spp.</i>		0.03
Family Muridae		0.01
<i>Mus musculus</i>		0.01
<i>Rattus norvegicus</i>		0.02
<i>Rattus rattus</i>		0.01
<i>Rattus spp.</i>		0.04

Family Dipodidae		<0.01
<i>Napaeozapus insignis</i>		0.03
<i>Zapus hudsonius</i>		0.01
Family Sciuridae		
<i>Sciurus carolinensis</i>		0.03
Unidentified Rodentia		0.08
Unidentified mammal	0.28	0.28
Reptile	0.01	
Order Squamata	0.01	0.01
Shellfish	0.35	
Order Amphipoda	0.01	
Family Talitridae		<0.01
Unidentified Amphipoda		<0.01
Order Decapoda	0.29	
<i>Emerita talpoida</i>		0.01
<i>Libinia emarginata</i>		0.02
<i>Ocypode spp.</i>		<0.01
Unidentified Decapoda		0.27
Unidentified shellfish, Class Bivalvia	0.01	0.01
Unidentified shellfish, Class Malacostraca	0.03	0.03
Unidentified shellfish, class unknown	0.03	0.03
Vegetation	0.76	
Fagales	0.02	
Family Fagaceae		0.02
Poales	0.09	
Family Poaceae		0.09

Rosales		0.02	
<i>Prunus maritima</i>			0.02
<i>Prunus spp.</i>			<0.01
Unidentified vegetation		0.65	0.65
Unknown	0.23	0.23	0.23

Bird remains were found in 35% of red fox scat samples. Many of those remains were unidentifiable past Class Aves (24% of samples). Of those that were further identifiable, Anseriformes (ducks, geese, swans, and similar waterfowl; 6% of samples), Passeriformes (perching birds, including songbirds; 6%), and Charadriiformes (waterbirds, including gulls, terns, plovers, 3%) were the most common orders. We did not find any identifiable piping plover remains in red fox scats.

We found anthropogenic items in 16% of red fox scat samples. These items included aluminum foil, paper, polystyrene, stickers, chewing gum, plastic packaging, part of a plastic bottle lid, small glass fragments, and scented candle wax.

Mammals were the most frequently occurring prey item category in domestic cat scats (3/3 samples), followed by birds (2/3), insects/arachnids (2/3), and vegetation (2/3). Insects/arachnids (2/2 samples); mammals (1/2) were the most frequently identified prey in domestic dog scats. The only definitive piping plover remains found in our diet analyses included one set of adult leg bands and Charadriidae feathers found in a domestic cat scat sample collected at Smith Point County Park in June 2018.

Seasonal diet comparisons from scat samples

Frequencies of occurrence in scat samples were similar between seasons for anthropogenic ($\chi^2_1 = 1.25$, $P = 0.26$), fish ($\chi^2_1 = 0.18$, $P = 0.67$), mammal ($\chi^2_1 = 2.57$, $P = 0.11$), shellfish ($\chi^2_1 = 0.02$, $P = 0.88$), vegetation ($\chi^2_1 = 0.00$, $P = 0.97$) and unknown ($\chi^2_1 = 1.35$, $P = 0.25$) categories (Figure 47). Frequency of occurrence of bird remains in scat samples was significantly higher in Fall/Winter than Spring/Summer

($\chi^2_1 = 12.89$, $P < 0.001$), and frequency of occurrence of insect/arachnid remains was significantly higher in Spring/Summer than Fall/Winter ($\chi^2_1 = 23.49$, $P < 0.001$). Reptile remains were excluded from our seasonal comparison analyses since no reptile remains were found in samples collected in spring/summer.

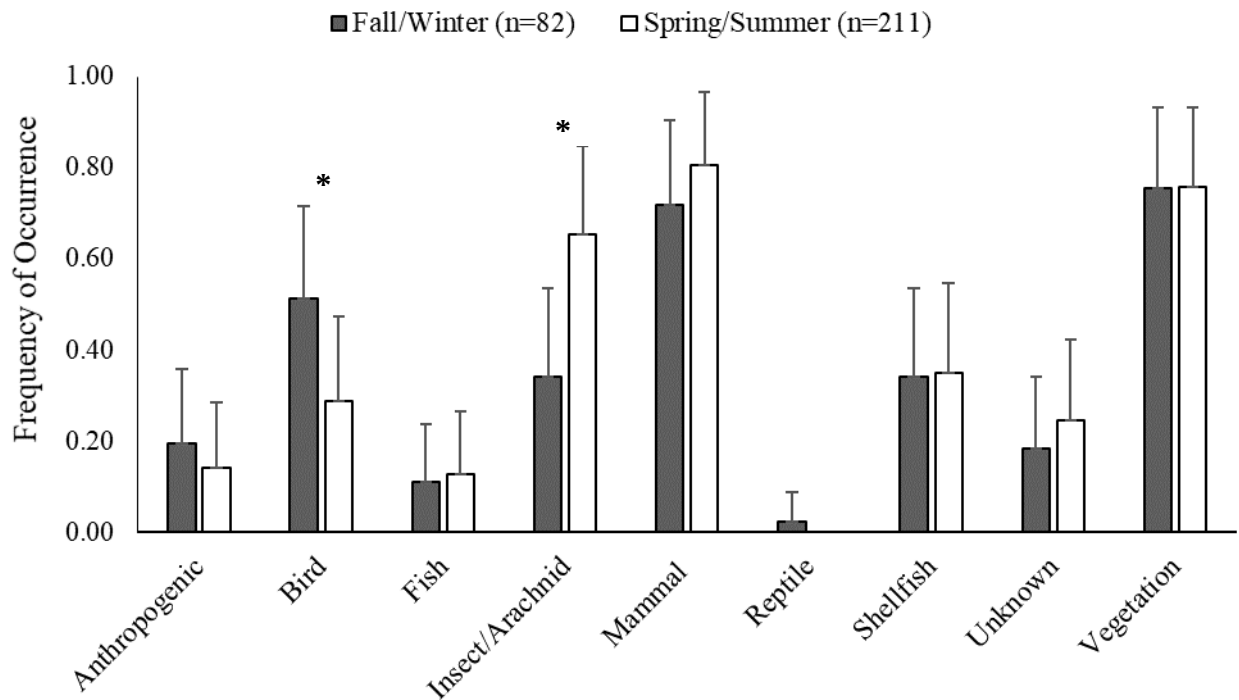


Figure 47. Seasonal comparison of frequency of occurrence by scat sample, defined as the proportion of scat samples that contained at least one item in a given category, for broad categories of food items found in fecal dietary analysis of red fox scat samples ($n = 223$) collected opportunistically, during systematic surveys, and at den sites on Fire Island, New York in 2016–2019. Error bars indicate upper 95% confidence intervals. * indicates Pearson’s chi-square $P < 0.05$ between seasons.

Individual diet comparisons

Seventy-one of the 267 scat samples sent to the MECU contained sufficient DNA to yield an individual red fox identification via genotyping analyses. We detected 48 unique individual genotypes, with 1-5 scat samples traced back to each individual. For the 3 red foxes for whom >3 scat samples were collected, we identified an average of 6.67 ± 0.62 SE different categories of prey consumed,

11.33 $\pm$ 1.03 SE different orders, and 12.33 $\pm$ 1.03 SE different species/lowest identifiable taxonomic levels consumed per individual (Table 48).

Table 48. Number of scats collected opportunistically, during systematic transect surveys, and at den sites from each genetically-identified red fox (n = 13 scats, n = 3 unique red foxes) on Fire Island, New York in 2016–2019, that contained at least one prey item from a given order. If prey items could not be identified to order, the lowest identifiable taxonomic level or categorical description is reported. The total number of scats traced back to each fox via microsatellite genotyping analyses is shown in parentheses. Only foxes for which >3 scats were found are included in this table.

Order	Fox		
	Male-1 (n=4)	Male-2 (n=5)	Female-1 (n=4)
Order Anseriformes		1	
Anthropogenic	3	1	
Order Artiodactyla	2		
Order Charadriiformes			1
Order Chiroptera	1		
Order Coleoptera		3	1
Order Decapoda	1	1	
Order Didelphimorphia	1		
Order Lagomorpha			1
Order Poales	1		
Order Rodentia	3	2	2
Order unknown, Class Insecta		2	2
Order unknown, Class			
Malacostraca	1		
Unknown avian	2	2	1
Unknown fish		1	
Unknown mammal	1	2	3
Unknown reptile	1		
Unknown vegetation	1	3	4
Unknown	1	2	1

Den monitoring and prey item surveys

We monitored 26 active breeding dens (n = 15 natal dens, 11 secondary dens) during our monitoring activities from April–August 2016 and 2017 and recorded prey remains outside of 18 of

them (n = 13 natal dens, 5 secondary dens). Dens without prey remains or food items in the vicinity (n = 8) were generally those used later in the season (after late May) and were excluded from our diet analyses, but they were included in comparisons of litter size relative to proximity to development. Due to sarcoptic mange outbreaks on the island, very few red foxes were present in the study area in 2018, and we found no breeding dens or evidence of successful reproduction during the 2018 breeding season (Part 3, Section 1).

Fish (89% of dens with food items), shellfish (67%), and mammal (67%) remains were found outside the highest proportion of dens (Table 49). Of the total items recorded outside of dens, fish (51% of items) and shellfish (27%) made up over 75% of total prey remains found. We identified 13 different orders of prey items outside of dens. Of these, Rajiformes (flattened cartilaginous fish, 89% of dens with food items) and Venerida (bivalve mollusks, 67%) were found outside the highest proportion of dens, and made up 61% of all food items recorded (Table 49). This pattern held true at the lowest identifiable taxonomic level, with skates (Family Rajidae, 89% of dens with food items) and Atlantic surf clams (*Spisula solidissima*, 67%) representing all observed items within orders Rajiformes and Venerida, respectively (Table 49). White-tailed deer remains also were frequently found (50% of dens with food items), but totaled only 3% of recorded items. We found bird remains outside of 44% of dens with food items; gulls (*Larus spp.*) were the most common, recorded at 17% of dens with food items but comprising only 1% of all recorded items at dens.

We found a variety of anthropogenic food remains and/or inedible items outside of 50% of dens with food items. These anthropogenic items made up 12% of all items recorded and included fast-food bags and wrappers, chip bags, granola bar and candy wrappers, empty drink cups and bottles, a cat food can, plastic forks, napkins, and a tube of antibacterial ointment.

Table 49. Frequency of occurrence by den ('Den' columns), defined as the proportion of dens (n = 18 dens) outside of which at least one item in a given category was recorded, and frequency of occurrence by item ('Item' columns, n = 278 prey items), defined as the proportion of all counted items belonging to a given category, for all prey remains and food items found during den prey item surveys on Fire Island, New York in 2016–2017. Results are presented by general category, taxonomic order, and species/lowest identifiable taxonomic level (for items that were not identifiable to species). These results do not include any items that were found in scats collected outside of dens, which were analyzed separately.

Item classification	Category		Order		Species/lowest identifiable level	
	Den	Item	Den	Item	Den	Item
Anthropogenic	0.50	0.12	0.50	0.12	0.50	0.12
Bird	0.44	0.04				
Order Anseriformes			0.06	<0.01		
Family Anatidae					0.06	<0.01
Order Charadriiformes			0.17	0.01		
<i>Larus spp.</i>					0.17	0.01
Unidentified avian			0.22	0.02	0.22	0.02
Fish	0.89	0.51				
Order Rajiformes			0.89	0.38		
Family Rajidae					0.89	0.38
Order Scorpaeniformes			0.11	0.01		
<i>Prionotus spp.</i>					0.11	0.01
Order Squaliformes			0.11	0.02		
<i>Squalus acanthias</i>					0.11	0.02
Unidentified fish,			0.39	0.09	0.39	0.09
Superclass Osteichthyes						
Mammal	0.67	0.06				
Order Artiodactyla			0.50	0.03		

<i>Odocoileus virginianus</i>				0.50	0.03	
Order Carnivora		0.11	0.01			
<i>Procyon lotor</i>				0.11	0.01	
Order Rodentia		0.17	0.01			
<i>Peromyscus spp.</i>				0.06	<0.01	
<i>Sciurus carolinensis</i>				0.11	0.01	
Unidentified Rodentia				0.06	<0.01	
Unidentified mammal		0.11	0.01	0.11	0.01	
Reptile	0.06	<0.01				
Order Testudines		0.06	<0.01			
<i>Malaclemys terrapin</i>				0.06	<0.01	
Shellfish	0.67	0.27				
Order Decapoda		0.11	0.01	0.11	0.01	
Order Littorinimorpha		0.06	0.01			
Family Naticidae				0.06	0.01	
Order Mytilida		0.11	0.01			
<i>Geukensia demissa</i>				0.11	0.01	
Order Venerida		0.67	0.23			
<i>Spisula solidissima</i>				0.67	0.23	
Unknown	0.06	<0.01	0.06	<0.01	0.06	<0.01

Proximity to development, anthropogenic food waste at dens, and red fox litter sizes

Neither the accumulated human food waste per day nor fish remains per day were significantly correlated with proximity to development (Spearman's rank correlation coefficient: $\rho_{16} = 0.02$, $P = 0.93$, $n = 18$ for human food waste; $\rho_{16} = 0.11$, $P = 0.67$, $n = 18$ for fish remains). Litter sizes at both natal and secondary dens were not significantly correlated to proximity to development (Spearman's

rank correlation coefficient: $\rho_{13} = -0.37$, $P = 0.17$, $n = 15$ for natal dens; $\rho_9 = 0.41$, $P = 0.21$, $n = 11$ for secondary dens), nor the accumulated human food waste per day (Spearman's rank correlation coefficient: $\rho_{11} = 0.29$, $P = 0.33$, $n = 13$ for natal dens; $\rho_3 = 0.35$, $P = 0.56$, $n = 5$ for secondary dens). The accumulated number of fish remains per day was significantly positively correlated to litter sizes at secondary dens (Spearman's rank correlation coefficient: $\rho_3 = 0.95$, $P = 0.01$, $n = 5$), but only marginally positively correlated with litter sizes at natal dens (Spearman's rank correlation coefficient: $\rho_{11} = 0.52$, $P = 0.07$, $n = 13$).

Discussion

Red fox diets on Fire Island were highly varied and included a wide range of natural and anthropogenic food items. Our finding that mammals formed a key portion of red fox diets on Fire Island is in line with the previous descriptions of red fox diets on barrier islands.

On Assateague Island, MD, Krim et al. (1990) found mammal remains in 87% of scat samples collected in May–August, compared to our observation of mammal remains in 78% of scat samples collected during our Spring/Summer surveys, which were conducted in April–August. However, our observed frequencies of occurrence for species were different. Krim et al. (1990) found cottontail rabbit (*Sylvilagus floridanus*), meadow vole (*Microtus pennsylvanicus*), and white-footed mouse (*Peromyscus leucopus*) were the most frequent mammal species represented, occurring in 44.4%, 31.5%, and 24.1% of scats, respectively, and they did not identify any other mammal remains to species. For comparison, white-tailed deer, unidentified voles (*Microtus spp.*), and cottontail rabbits were the most common mammalian prey species in our study, occurring in 12%, 9%, and 8% of scats, respectively, although a significant proportion of mammalian remains found in our analyses, particularly bone fragments and hairs, were not further identifiable (28% of samples). While cottontail rabbits, meadow voles, and white-footed mice were among the mammalian prey recorded our study, each of these species occurred in $\leq 8\%$ of our scat samples. In their previous study of fox diets on Fire Island, Peterson et al. (2020) found voles in 32.2% of samples collected throughout 2011 and 2012, a frequency more similar to that reported by Krim et al. (1990). They also found cottontail rabbit

remains in 15.6% of samples and white-footed mouse remains in 4.4% of samples, roughly twice as often as we found these species in samples collected in 2016–2019.

The frequent presence of white-tailed deer remains in scat samples (12% of scats) and at more than half of dens with food items was surprising, given their large size in comparison to other major prey items. Peterson et al. (2020) also found white-tailed deer remains in scat samples, but less frequently (4.4% of samples). Red fox predation on fawns has been described previously, but is generally thought to be infrequent and limited to times of year when fawns are less mobile (Epstein et al. 1983). We found deer remains in red fox samples collected in almost all months of the year when we conducted transect surveys, which would suggest that these occurrences for the most part reflect scavenged carcasses. We frequently encountered deer carcasses and remains while conducting our transect surveys, both in situ and moved to areas out of public view by park staff. Many of these deer died from wildlife-vehicle collisions, which were common in parts of the study area. We recorded both fawn and adult deer remains during our den surveys. We also received an anecdotal report of a red fox dragging a wounded fawn into the bushes at the edge of a parking lot, presumably during an attempted predation event (Samantha Robinson, [Virginia Tech, Blacksburg, VA], personal communication, [July 2020]). White-tailed deer are abundant on Fire Island, with estimated densities of 25-35 deer/km², and even higher local densities in some areas, reported in recent surveys (Underwood 2005, Kilheffer et al. 2019).

A major difference between our study and the 2 prior studies of red fox diets on barrier islands is the lower frequency at which we found bird remains in scat samples. Krim et al. (1990) and Peterson et al. (2020) reported bird remains in 46.3% of scat samples and 43.3% of scat samples, respectively, compared to our observation of bird remains in only 35% of samples. Although this difference is not that large, the contrast becomes more apparent when broken down by order and family. Similar to Peterson et al. (2020), we found passerine birds remains most often in scats, but at a much lower frequency, with their study reporting a 22.2% of samples containing passerine remains compared to the 6% of samples in which we observed remains from this order. As with their study, Anseriformes

and Charadriiformes were our most next commonly found bird orders, but at slightly lower frequencies (6% and 3% of samples, respectively, in this study vs. Family Anatidae remains found in 10.0% of samples and Family Laridae remains found in 11% of samples in their study). Krim et al. (1990) did not report a further taxonomic breakdown in their results. The high proportion of bird remains that we were unable to identify further (24% of samples) may have contributed to these discrepancies in results between the two studies.

Despite likely red fox predation of nests at Smith Point County Park in 2015 (Monk et al. 2015) and observed red fox disturbances at nest exclosures in 2018 (Hermanns et al. 2018), we did not find any clearly identifiable piping plover remains, and relatively few remains identifiable to Family Charadriidae (1% of samples), in our examination of red fox scat samples collected in 2016–2019. In addition to piping plovers, 2 other members of Family Charadriidae (semipalmated plovers [*Charadrius semipalmatus*] and black-bellied plovers [*Pluvialis squatarola*]) are present in our study area during the month (June) in which those samples were collected (Monk et al. 2020). We found items resembling egg shells in 3 scat samples, but could only confidently identify them as bird egg shell remains in one instance. Those particular egg shell remains were blue in color, ruling out the possibility of them having come from piping plover eggs.

Peterson et al. (2020) similarly found no piping plover remains in suspected red fox samples collected in 2011–2012. This lack of remains in scat suggests that red fox predation of piping plover adults and chicks is opportunistic and variable across years, as opposed to habitual, targeted hunting. It also suggests that increases in piping plover abundance on the island in between the 2 studies have not translated to increases in plover predation events as detectable in feces. For context, the number of breeding piping plover pairs on Fire Island and the western portion of Westhampton Island nearly doubled between the conclusion of Peterson et al.'s (2020) data collection and the conclusion of this study, with 30 breeding pairs in 2012 and 58 breeding pairs in 2018 (Walker et al. 2019). While direct predation by red foxes on piping plover adults and chicks may not be a frequent occurrence on the island, infrequent predation still may impact the plover population. In addition, indirect effects of red

fox presence and disturbance may have sub-lethal negative effects on piping plovers, warranting further investigation. For example, piping plover chick survival during this study, based on concurrent monitoring, was negatively correlated with red fox trap success (Robinson 2020). Previously, Doherty and Heath (2011) found the number of red fox tracks counted on nearby transects to be the strongest predictor of piping plover nest abandonment at several sites across Long Island, NY, including in part of our study area.

Although our analyses for non-fox samples were limited in scope, the discovery of adult piping plover leg bands in a domestic cat scat sample highlights the potential impacts of free-ranging cats in shorebird nesting areas and the potential need for including domestic cats in predator management considerations. Both nest abandonment and loss of chicks have been attributed to feral cats previously on Fire Island (Winter and Wallace 2006). Moreover, on adjacent Westhampton Island, feline depredation of piping plovers and nests and nest abandonment, have been reported (Winter and Wallace 2006, Cohen et al. 2009).

Red fox consumption of most food categories was consistent across seasons, but bird and insect/arachnid consumption varied seasonally, contrary to our initial hypothesis that red foxes would respond to the seasonal influx of piping plovers and other breeding shorebirds with increased consumption of avian prey in Spring/Summer. This pattern could reflect changes in the availability of other bird species that occurred more commonly in red fox diets, such as ducks and passerines. For insects/arachnids, the higher frequency of occurrence in Spring/Summer compared to Fall/Winter (65% vs. 34% of samples) may be related to differences in abundance due to seasonal die-offs and hibernation. Peterson et al. (2020) did not observe any significant differences in dietary composition among seasons, and did not report finding any insect/arachnid remains in red fox scats. Conversely, O'Connor et al. (2020) observed similar seasonal differences in insect consumption in their study of red fox diet in coastal Queensland, Australia, with summertime increases in Christmas beetle (*Anoplognathus spp.*) availability likely driving the trend.

Some prey items may be underrepresented in our fecal dietary analysis results as compared to den prey item surveys due to a lack of identifiable remains following digestion. For example, skates (Family Rajidae) were the most frequently found item at dens (89% of dens with prey remains) and made up 38% of all prey items recorded during den surveys, but were not found in any samples examined in our fecal dietary analyses. Anthropogenic food items may be similarly underrepresented in scat samples, as our ability to detect consumption is based on detection of wrappers and associated waste, which may not accompany or be consumed along with all food items. We found anthropogenic items in 14% of scat samples collected during the Spring/Summer season, but at 50% of red fox dens with prey remains. The application of more advanced laboratory methods may help overcome these detectability limitations in future work. For example, stable isotope analysis has been used to specifically examine anthropogenic food consumption of red foxes in other systems influenced by urbanization (e.g., Handler et al. 2020, Meckstroth et al. 2007). Similarly, DNA metabarcoding could be used to examine consumption of prey items that may not be detected during fecal analyses, such as cartilaginous fish (Pompanon et al. 2012).

The repeated occurrence of anthropogenic items in red fox scats and at dens suggests that red foxes are regularly exploiting these additional food resources. In our fecal analysis results, anthropogenic items occurred more frequently than any single genus or species of prey item that we recorded. Interestingly, we did not see a significant difference in the frequency of occurrence of anthropogenic items in scat between seasons, despite seasonal differences in the number of people present in our study area. This frequent, year-round occurrence suggests that anthropogenic food items are readily available even when fewer visitors are using the parks. We observed regular feeding of red foxes and other wildlife in the study area, despite signs discouraging this behavior. These findings differ from those of Peterson et al. (2020), who found no evidence of anthropogenic food consumption in their study. These differences could be due to the fact that our surveys covered all passable habitats, multiple park areas, and a longer period, resulting in a larger overall sample size (300 scats vs. Peterson et al.'s (2020) 90 scats) and more potential opportunities to detect

anthropogenic foods in scats. It could also reflect possible shifts in anthropogenic food consumption by foxes on the island over time, as their data collection ended in 2012 and ours began in 2016. In line with Peterson et al.'s (2020) findings, O'Connor et al. (2020) found anthropogenic food waste infrequently (4.3% of samples) in red fox scats collected in developed coastal Queensland, hypothesizing that good waste management practices were a contributing factor in the Queensland study.

In addition to the anthropogenic foods that humans may be providing to the red fox population, we believe that a large portion of the fish found in scats and dens may have come from discarded angler bycatch, as Krim et al. (1990) suspected of fish remains found outside of fox dens on Assateague Island. In our study area, skates (Family Rajidae), dogfish (*Squalus acanthias*), and other non-target species are often thrown up onto the beach rather than back into the ocean, making these food resources readily accessible to red foxes and other terrestrial species. It is also possible that fish thrown back into the ocean following landings may later die and wash up on the beach, thus becoming accessible to scavengers. For example, Capizzano et al. (2016) reported an average discard mortality rate of 16.5% of Atlantic cod (*Gadus morhua*) when using typical catch-and-release angler equipment and methods, with the majority of post-capture mortalities occurring ≤ 16 hr following release.

The lack of significant correlation between proximity to development and human food waste accumulation at dens was surprising. We found anthropogenic food items outside of several dens in the undeveloped wilderness area, where backcountry camping was allowed along much of the shoreline. These observations suggest that proximity to development alone may not fully explain differences in anthropogenic food availability across the island. We recommend considering other indices of anthropogenic food availability, such as daily visitor counts, surveys on wildlife-feeding/waste management habits, or conducting transect surveys to record available foods (e.g., Contesse et al. 2004), in future studies.

While we did not find clear evidence that proximity to development or the rate of human food waste accumulation at dens are correlated with larger litter sizes, our comparisons suggest that the rate of fish remains accumulation at dens may positively influence litter sizes. This correlation indicates that fish may represent an important food source for kits. However, more information is needed to determine what proportion of these remains were scavenged from natural ocean wash-up at wrack lines vs. angler discards.

Estimated litter sizes are only one of many possible metrics that could be used to investigate the effects of anthropogenic resources on the island's red fox population. In addition to influencing reproductive output (e.g., Beckman and Lackey 2008), previous research has shown that anthropogenic food subsidies may affect predator populations by influencing relative abundance in an area (e.g., Shapira et al. 2008), individual survival rates (e.g., Bino et al. 2010), or even body mass and morphometric measurements (e.g., Stepkovitch et al. 2019). Anthropogenic food subsidies also may influence population density by influencing home range sizes, thus affecting the number of individuals that a given area can support. For example, Main et al. (2020) found that red foxes in areas of higher human population density had smaller home range sizes. We recommend further monitoring into the effects that anthropogenic food resources may have on the red fox population on Fire Island, as it is possible that these items may be subsidizing the diets of foxes or influencing other aspects of fox ecology in our study area. If so, these resources may be indirectly influencing red fox interactions with piping plovers and other species of concern.

Section 5: Use information collected in objectives to make recommendations on utility of, and recommend methodologies for, management of red fox populations in the study area and in other coastal habitats.

This section describes the following objective for red fox monitoring associated with the Fire Island Inlet to Moriches Inlet Fire Island Stabilization Project:

Objective 6: Utilize information collected in objectives 1–5 to make recommendation on utility of, and recommended methodologies for, management of red fox populations in the study area and in other coastal habitats.

Red foxes (*Vulpes vulpes*) were important predators of piping plovers on Fire Island during our monitoring activities from 2015–2019. Red fox population dynamics, spatial ecology, and impacts on piping plovers varied dramatically across the monitoring period and were driven by high mortality and partial extirpation caused by sarcoptic mange infections. At the outset of this monitoring plan, we had expected to monitor the effects of predation management, as implemented by land managers, on red fox populations and piping plovers. Only one red fox was lethally removed during the monitoring period by USDA Wildlife Services at Smith Point County Park in the Winter of 2015–2016. This removal was in response to high plover nest mortality caused by likely one or a few foxes in 2015. A single red fox was removed near the end of the die-off of foxes at that site due to the mange outbreak. Non-lethal predator exclosures around piping plover nests were widely deployed and found to be the most important predictor of piping plover nest survival. Thus, even though sarcoptic mange did drive the population dynamics of red fox, the findings here are still highly informative to ongoing decisions about both non-lethal and lethal predation management on both Fire Island and at other sites along the U.S. Atlantic Coast. In the sections that follow, we summarize our key findings from our monitoring activities and then apply those findings to help guide ongoing predation management options.

Direct impacts of red foxes and other predators on piping plovers

Red fox predation was a strong driver of piping plover reproductive output on Fire Island during portions of our monitoring period. In 2015, prior to the observed mange outbreak, 18 plover nests were believed to have been depredated by red fox at Smith Point County Park based on fox sign found at the nest site. At least one fox learned to enter exclosures at Smith Point by tearing the netting at the top to get to the eggs inside, leading to the removal of exclosures from nests, all of which all were subsequently depredated.

Two outbreaks of sarcoptic mange (caused by the *Sarcoptes scabiei* mite) then occurred over the remainder of the monitoring period, allowing us to better isolate the impacts of red fox on piping plovers in these sites. In some ways, the natural mange-outbreak acted as a pseudo-experiment on the effects of complete removal of foxes from a piping plover breeding area. Whether such management-driven extirpation of foxes would be feasible or recommended based on our findings is discussed below.

First, mange was detected in red foxes to the East of Old Inlet in late summer 2015; foxes were extirpated by mange and were apparently absent in that area from April 2016 to March 2017. Only sporadic sign from likely one individual was observed from April 2017 to the end of monitoring in 2019. Piping plover chick survival and overall reproductive output were negatively related to red fox trap success (an index of red fox activity based on the frequency of detections), such that plover chick survival and reproductive output were lower before versus after the mange die-offs. Our camera-based monitoring allowed us to simultaneously assess trap success of other known piping plover predators, but no relationship was found between feral cat or raccoon trap success and plover reproductive metrics. However, the bands of an adult piping plover were found in a feral cat scat, identified as such by genetic species-typing, at Smith Point County Park in 2018 after the mange-related die-off of red foxes at that site.

In 2016, prior to the mange-related die-off east of Old Inlet, red foxes were among the top 3 species captured on cameras deployed on piping plover nest exclosures throughout the study area.

However, in 2017-2019 and across all years of monitoring combined, humans, gulls, unknown or unidentifiable birds, and white-tailed deer were the most frequently detected species at exclosures. Thus, in no years were red foxes the most frequent visitor to nest exclosures as detected by nest cameras.

Prior to, and during the mange-related die-offs of foxes, we collected scat samples and catalogued prey remains around den sites to quantify red fox diet and assess the role of piping plovers in their diet. Red foxes on Fire Island, NY in 2016-2019 had a highly varied diet. At the broad categorical level, mammals (75%), vegetation (73%) and insects (55%) were found in the highest percentage of samples examined. We identified 27 unique taxonomic orders of prey items. We did identify Charadriiformes remains in 3% of scat samples, but were unable to identify any prey remains down to the level of the piping plover, as the degradation of the feather remains after gut passage prohibited species-level identification. In analyses of 297 confirmed or probable red fox scat samples collected from 2016 –2019, no bands of piping plovers were found. However, piping plover bands were found in 1 of 3 feral cat scat samples.

In 2018, we captured photos of a peregrine falcon on a nest camera less than an hour before the carcass of one of the incubating adults was found inside the same exclosure. In 2019, a peregrine falcon was seen eating a plover chick while on its associated nest's exclosure, and the flagged leg of an adult was found at the base of the same exclosure less than a week later. Given how often we observed peregrine falcons on or near exclosures while surveying, we expected more camera detections than what were observed. Given these observations, plus the frequency of observations of gulls and other avian predators on nest cameras, additional monitoring and management of avian predators may be warranted.

Indirect impacts via habitat use, spatial overlap and behavior of red foxes and piping plovers

In addition to the quantifying the direct predation impacts of red foxes and other predators on piping plovers, we explored shared habitat use, spatial overlap and behavioral interactions as indirect metrics of predation risk by foxes on piping plovers and to best inform predation management.

Abundance and Density of Red Fox as Indirect Indicators of Risk

As noted above, the mange outbreak was the largest source of mortality for all marked red foxes and drove dramatic population declines and reproductive failure of foxes across our monitoring period. We quantified four lines of evidence documenting the change in red fox populations and the relation to the mange outbreaks. First, red fox camera trap success, which is an index of relative activity, declined dramatically in our remote camera grid surveys following the mange outbreaks in each monitoring area (Smith Point County Park and Old Inlet East: 13.99 Trap Success (TS) pre-mange in 2015-2016 to 5.08 TS in 2018-2019; Robert Moses State Park: 119.95 TS pre-mange in 2016-2017 to 4.99 TS post-mange in 2018-2019; Fire Island National Seashore Watch Hill to Old Inlet 103.36 TS pre-mange in 2016-2017 to 8.30 TS in 2018-2019). Second, red fox density, as quantified from both GPS-collared and ear-marked individuals and counts at den sites, declined dramatically following the mange outbreaks in each monitoring area (Smith Point County Park and Old Inlet East, post-mange data only, 0 foxes/km² in 2016, 0.21 foxes/km² in both 2017 and 2018; All areas west of Old Inlet, 5.88 foxes/km² in 2016, 3.48 foxes/km² in 2017 and 0.42 foxes/km² in 2018). Third, we saw similar declines following the mange outbreak in the number of unique genotypes detected in scat samples collected during twice regular transect sampling, from 32 unique individual genotypes in 2016 to 14 in 2018–early 2019. Fourth, we saw a decline in reproduction by foxes following mange outbreaks and a complete reproductive failure of red foxes in 2018 (17 dens and 8 family groups monitored in 2016 to 0 in 2018). All of these metrics combined quantify the collapse of red fox populations across the monitoring area and temporary extirpation of red fox in 2016 at Smith Point County Park; thus, red fox predation risk to plovers dramatically decreased as the monitoring progressed. As of the end of

monitoring in early February 2019, we suspect only one fox was present to the east of Old Inlet. As of this same time, no red fox were observed to the west of Old Inlet. We suspect the red fox will recolonize Fire Island, and it will be important to both monitor the recolonization and consider recolonization dynamics in future predation management efforts.

The densities of red foxes observed in our monitoring areas before the mange outbreaks were similar to those found in urban areas where foxes were heavily subsidized by anthropogenic food sources. Similar to urban fox populations, we found heavy use of anthropogenic food sources (15% of scat samples and 63% of den locations had anthropogenic food remains), even in the most remote parts of the Fire Island National Seashore Wilderness Area, near Old Inlet West. It is likely that these human food subsidies contributed to high population densities of foxes, and active management of these subsidies should be considered in future predation management efforts in order to minimize fox densities and impacts to piping plovers.

Occupancy as an indicator of risk independent of abundance and density

Whereas indices of fox activity, fox abundance and density, and fox reproductive output all declined dramatically pre- to post-mange, red fox occupancy (i.e., probability of presence accounting for detection) remained high except during the window of fox extirpation in areas east of Old Inlet. For example, at Smith Point County Park, red fox occupancy was 0.86 in 2015-2016 before mange, 0 in 2016-2017, and 0.84 and 0.80 in 2017-2018 and 2018-2019. In the latter two years, trapping efforts and examination of photos led us to conclude that there was likely only 1 fox east of Old Inlet, yet that fox was present at 84% and 80% of camera stations over the monitoring area. Similarly, red fox occupancy was 1 at both Robert Moses State Park and Fire Island National Seashore, west of Old Inlet, in 2015-2017. Thus, red foxes were present at every camera station in those monitoring areas. Even after the mange-related declines in abundance, density and reproduction in these areas west of Old Inlet in 2017-2019, occupancy remained high (0.82 at Robert Moses State Park, 0.86 Fire Island National Seashore). Thus, despite dramatic population declines caused by mange, and reproductive

failure in 2018-2019, we found red foxes were present across the monitoring areas at rates similar to before the mange impacts. These results, along with the habitat selection and home range behaviors of foxes described below, suggest that predation risk for piping plovers persists even at very low red fox population sizes.

Habitat and spatial overlap of red foxes and plovers

Our ability to track individually-marked and GPS collared red foxes was unique, and has never been conducted in a coastal or barrier island system. Our findings of high population density, as described above, were related to relatively small home ranges and core use areas for resident, breeding foxes. The home range sizes of resident, breeding foxes in our monitoring area were similar to other urban fox populations with high food subsidies. However, we also found that season and sex were strong drivers of home range sizes and movement patterns in red fox.

Males dispersed in the fall and transient, non-breeding and non-territorial males were present across the years and monitoring areas. Both dispersing and non-breeding males had very large home ranges, frequently moving between Old Inlet and both Moriches and Fire Island Inlets. However, no marked foxes were observed to cross Old Inlet. The observed dispersal and transient behavior of male red foxes suggests a high capacity for dispersal and recolonization should an occupied territory become available. These transient animals regularly moved between management areas, with most transient animals traveling the entire length of the island available to them. Thus, any predation management, lethal or non-lethal, must consider this recolonization potential and be sustained in its deployment.

Foxes on the island appear to be selecting areas closer to vegetation and wet sand edges, potentially including bayside marsh habitats, for daytime resting periods, while selecting more open habitats for nighttime periods of higher activity and movement. The fact that resident foxes used areas closer to vegetation, on average, while transients used areas further from vegetation, supports this idea of differential habitat use for movement. Hinton et al. (2015) found similar differences in

selection for vs. against roads in transient coyotes compared to residents, and hypothesized that either more efficient movement paths or increased ability to detect residential animals and their territory boundaries could explain this difference in selection.

Within restoration areas, predicted relative suitability for inclusion in home ranges was generally higher for males, and was higher for both sexes in New Made (6.43 out of 10, 10 being highest suitability) compared to Great Gun (5.80 out of 10) due to differences in vegetation and open sand between the two. At Great Gun, suitability was highest along the main dune and in areas closest to vegetation. Similarly, suitability at New Made was highest in more vegetated areas. Both of these restoration areas were relatively more suitable than not (i.e., > 5 suitability). Continued vegetation removal and management will decrease suitability of the sites for daytime resting and also minimize the ability of concealment by foxes, and should be considered as part of a non-lethal management toolkit.

Behavioral responses of red fox to piping plovers

Nest exclosures should continue to be used, as they were demonstrated to be the strongest predictor of piping plover nest success. Further, we did not find evidence that GPS-collared red foxes were attracted to the exclosures in the 48 hours after setup, pipping or hatching. However, in 2015, a fox learned how to climb into and depredated nests in exclosures at Smith Point County Park. When managers subsequently removed the remaining exclosures throughout the park, those nests were immediately destroyed.

When foxes learn to enter exclosures, we think that the most effective management measure would be a targeted removal of the offending red fox, which also would protect chicks to some degree. In a high density red fox population, as was present before the mange outbreak, most resident red foxes maintained a home range with radius of about 1.4 km (in narrower sections of island which averaged 150m ocean to bay width) or 523 m (in wider island sections which averaged 400m ocean to bay width). Therefore, removal of exclosures within that radius (either about 1.4 km in

narrow island portions or 500 m in wide sections) might prevent adult plovers from interacting with foxes at exclosures, but likely would result in egg loss. Removal of exclosures from an entire management area may result in large-scale nest failures without reducing adult-fox interactions outside of the home range of the offending fox.

An extensive review of the adaptive process and options of lethal and non-lethal techniques for predation management is provided in Guidance and Best Practices for Coordinated Predation Management to Benefit Temperate Nesting Shorebirds (Hunt et al. 2019a). This document also recommends the use of a new tool, PiperEx, to further guide decisions about when to remove nest exclosures (Cohen et al. 2016). Currently, our data are not incorporated into the structured decision making process which guides PiperEx, but may be in future iterations and thus we recommend consideration of PiperEx alongside the recommendations summarized in this report. All predation management should be adaptive and collaborative between the land and predator managers as to the suite of options, and when possible, non-lethal techniques pursued before lethal.

We observed increased presence at exclosures and predation by raptors in later years of the monitoring. Further, gulls and other birds were the most frequent organisms, after humans, to be detected on camera traps deployed on nest exclosures. On the Missouri River, predation by great horned owls was density-dependent (Catlin et al. 2011a). It is too early yet to ascertain if that is the case on Fire Island, but we do recommend targeted monitoring of avian predators and their effects as piping plover density increases on Fire Island. Hunt et al. (2019) review and provide pros and cons of both lethal and non-lethal management options specific to avian predators.

Management of anthropogenic food sources

We found high occurrences of anthropogenic food remains in both scat samples and at den sites of red foxes. We also frequently observed people feeding red fox and other wildlife throughout the monitoring areas, despite official policies prohibiting such behavior. Human food subsidies are known to increase density of commensal predators such as red fox, and thus the availability of human

subsidies should be managed in order to reduce predation risk of red fox on piping plovers. We recommend that land managers on Fire Island consider launching a coordinated campaign to limit feeding of wildlife and to most efficiently manage trash from recreationists. Launching of a novel campaign now during the very low (east of Old Inlet) to potentially temporarily extirpated (west of Old Inlet) populations of red foxes could slow the population's rebound and thus continue to minimize predation risk. Under Best Practice 6, *Predation Management Outreach Tools* (Hunt et al. 2019a), communication best practices and examples of such are reviewed and related to predation management, in general. There are not yet any existing management campaigns related to food subsidies of predators along the Atlantic Flyway, so this task will be both a challenge for Fire Island managers and an opportunity for the entire flyway. Relevant discussion from Hunt et al. (2019) is quoted here for ease of access:

“Many public beaches feature anti-littering signs and signs prohibiting feeding of wildlife, but few, if any, connect this message to the problem of artificially inflated predator abundances in important shorebird nesting areas. Programs like the Crumb Clean campaign in the Redwoods National and State Parks (<https://www.nps.gov/redw/learn/nature/crumb-clean.htm>) and Leave No Trace (<https://lnt.org/>) are great examples of public outreach campaigns that target specific behaviors related to threatened species and conservation and preservation of natural areas, respectively. Similarly, the Fed Bear is a Dead Bear (<https://lnt.org/blog/fed-bear-dead-bear>) slogan is a popular campaign across the United States and may be a model for predation management messaging if adapted to local situations. However, some states have discontinued the use of this slogan as the public does not always understand that the garbage itself does not kill the bears, but rather the feeding-related habituation of bears leads to the need for lethal removal. Thus, further work is needed. At Crane Beach in Ipswich, MA, the management entity does deliver a leave no trace campaign and tells users that they must carry in and carry out all food and trash when using the beach (<http://www.thetrustees.org/about-us/press-room/press-releases/some-important-updates->

[from.html](#)); raccoon and skunk predation at the site is currently minimal (J. Denoncour, personal communication, Trustees).” - Hunt et al. 2019a

Harassment

Harassment may serve as an additional non-lethal management tool. Hunt et al. (2019a) describe several harassment techniques and considerations, including auditory and visual scare devices and chemical repellents that can be used to target specific predators. While these techniques can assist in frightening predators away from nesting areas and/or aid in aversive conditioning, there is the potential for habituation. In addition, some techniques may also frighten the target species for conservation away from nesting and foraging areas. Thus, it is important to carefully consider potential options and regularly re-assess the effectiveness of harassment efforts.

Similarly, targeted manipulation of behavioral responses may be used to influence the distribution and behavior of predator species. There is a growing body of scientific literature surrounding the “landscape of fear” concept (Laundré et al. 2010), which describes variation in space use due to differences in perceived risk, and potential applications to mitigate human-wildlife conflict. While the concept was originally applied to predator-prey interactions, it has recently gained attention in the study of human-wildlife interactions. For example, Suraci et al. (2019) found that pumas avoided areas where recording of human voices were broadcast during playback experiments, and moved more slowly in areas with speakers, indicating more cautious behavior. In the context of pest management, it has been suggested that managers can mimic different cues of predation risk or human presence to induce avoidance of a specific area, and/or manipulate behavioral responses of pest species. For example, Cromsigt et al. (2013) proposed the use of hunting to induce a fear response in ungulates and discourage use of areas in close proximity to people. This concept could potentially be extended to the management of foxes and other piping plover predators by mimicking the presence of competing predators or artificially inflating the perceived risk of human encounters in

a given area. As with more traditional harassment methods, it is important to ensure that these actions do not also elicit a fear response in target species for conservation.

Feral cat colonies and presence

We detected feral cats on camera stations every year (2015-2019) in every monitoring area on Fire Island. Further, we did find piping plover bands in 1 of 3 feral cat scats collected. We observed the general public maintaining discreet, and sometimes not discreet, feral cat structures at Smith Point County Park throughout the monitoring period, often near the parking areas and campgrounds. We did not observe such structures in Robert Moses State Park and Fire Island National Seashore, yet feral cats still were detected on cameras in every year of monitoring. We recommend prohibition of feeding of cats (and foxes) in all management areas in order to minimize population growth of these piping plover predators. Other management techniques (lethal removal, trap-neuter-release, TNR) often are controversial, but should be considered through collaborative discussions between land managers, predator managers, and the interested public in order to minimize predation risk to piping plovers by these non-native predators. In the development of the predation best practices document for the Atlantic Flyway (Hunt et al. 2019a), many managers mentioned the support of feral cat colonies in close proximity to beneficiary species as a major unaddressed challenge in need of a coordinated communications campaign. As in the case of development of a food subsidy reduction campaign, this will be both a challenge for Fire Island managers but a Flyway-wide opportunity if success can be achieved.

Vegetation management

We found proximity to vegetation to be a strong predictor of fox habitat selection, both within home ranges and across the landscape. Efforts to continue to minimize vegetation in areas used by

nesting piping plovers and their chicks will minimize both daytime rest site suitability and the potential concealment of foxes during hunting activities and other movements.

Lethal predation management options

Our findings on occupancy, home range use, and movements suggest that traditional lethal removal techniques may not be an efficient predator management option on Fire Island, given the frequency of transient individuals and regular movements between management units, unless conducted on an intensive level across the entire island. Lethal removal of red foxes, whether via shooting or trapping or fumigation of dens (see Hunt et al. 2019*a* for critiques of lethal options), is challenging and time-consuming. Unless extirpation is achieved, our data on movements suggest that recolonization of vacated territories will be rapid. Thus, we recommend deployment of the suite of nonlethal options mentioned above as the primary focus of predation management efforts. In the case of an individual fox learning to depredate nest exclosures, we first recommend consideration of non-lethal harassment options before lethal removal given the difficulty in ensuring that the ‘problem’ animal is the one lethally removed. As recommended consistently throughout Hunt et al. (2019*a*), we recommend land managers work collaboratively with USDA Wildlife Services or other professional predator management agencies or companies in adaptively developing and implementing management options.

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Appendix A. Supplementary tables for Part 2, Section 5: Compare the relative contribution of local growth (natal recruitment) vs immigration in population growth associated with new habitats 'Effectiveness monitoring and targeted studies in support of FIMI conservation measures.'

Table A-1. Model ranking results for the Barker (1997) survival model of true survival (S), and fidelity (F) for after-hatch-year (AHY) and hatch- year (HY) Piping Plovers on Fire Island, New York, USA (FNS), 2013–2019. Models shown are those with ≥ 0.01 model weight (w_i). For all models, resight rate (p), probability of emigrating and returning (F') were held constant, the supplementary period resight rate (R) was modeled as Age, the probability of being detected and dying during the supplemental period (R') was Age + Time and the rate of dead recoveries (r) was fixed at 0.

S	F	K	$\Delta AICc$	w_i	Deviance
HY:Year + Age	Age	22	0.00	0.54	555.07
Age+Year	Age	22	3.17	0.11	558.25
HY:Year + Age	Age + Year	27	3.20	0.11	548.09
Age	Age + Year	21	3.93	0.08	561.03
Age	Age	16	4.83	0.05	572.07
HY:Year + Age	HY:Year + Age	27	5.48	0.03	550.37
Age*Year	Age	28	5.69	0.03	548.54
Age	HY:Year + Age	21	6.91	0.02	564.02
Age + Year	Age + Year	27	7.69	0.01	552.59
Age + Year	HY:Year + Age	27	8.46	0.01	553.35

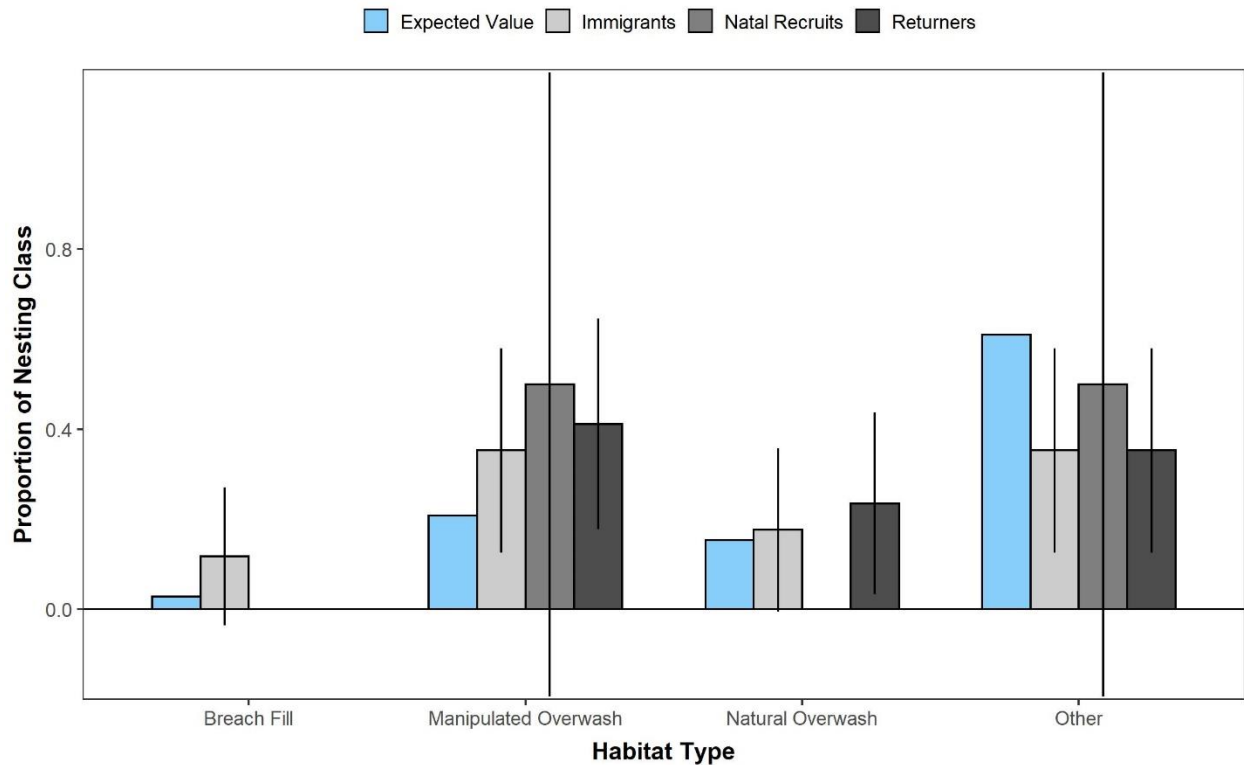


Figure A-1. Habitat used by immigrants, natal recruits, and returners in 2014 in relation to the expected usage based on availability of breach fill, manipulated overwash, natural overwash, and other habitats. Error bars represent the 95% confidence intervals and selection is evident when error bars do not overlap the expected habitat use value. (Immigrants: $\chi^2 = 8$, $P = 0.24$. Natal Recruits: $\chi^2 = 4$, $P = 0.26$. Returners: $\chi^2 = 12$, $P = 0.21$.)

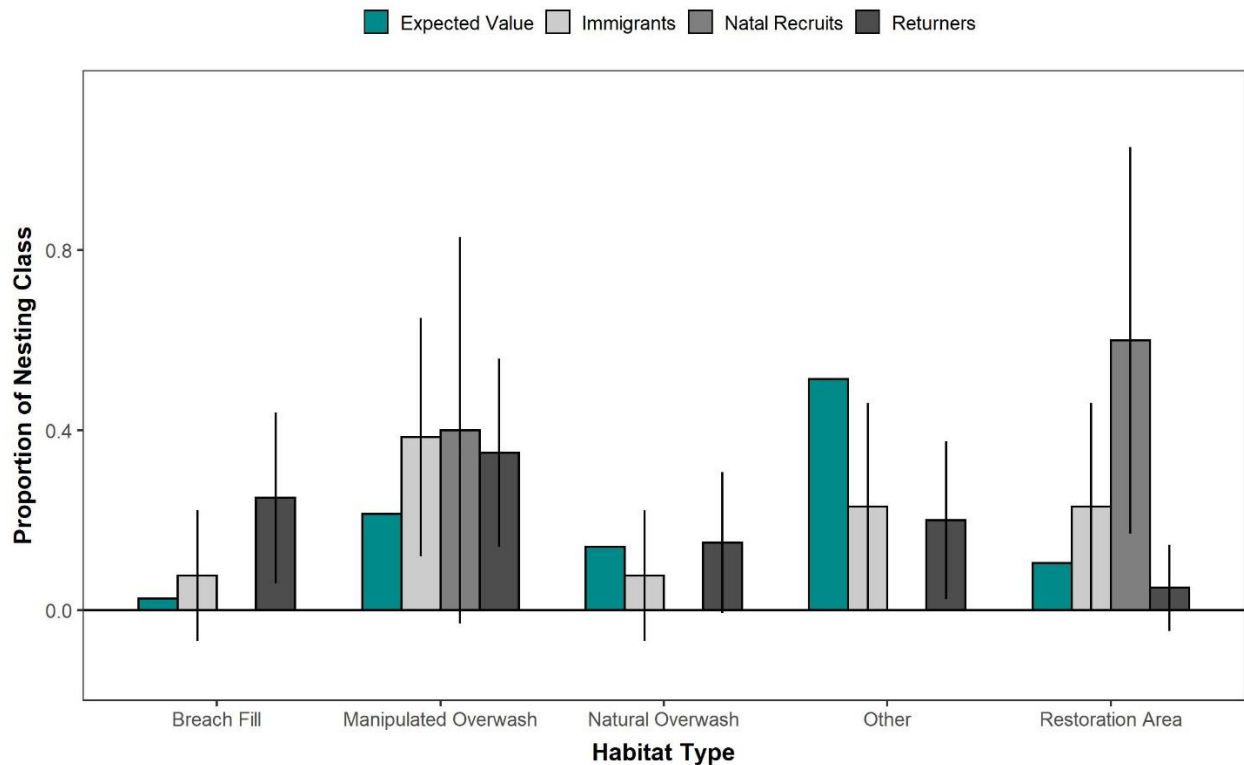


Figure A-2. Habitat used by immigrants, natal recruits, and returners in 2015 in relation to the expected usage based on availability of breach fill, manipulated overwash, natural overwash, other, and restoration area habitats. Error bars represent the 95% confidence intervals and selection is evident when error bars do not overlap the expected habitat use value. (Immigrants: $\chi^2 = 7.47$, $P = 0.11$. Natal Recruits: $\chi^2 = 15.83$, $P = 0.003$. Returners: $\chi^2 = 45.53$, $P < 0.001$.)

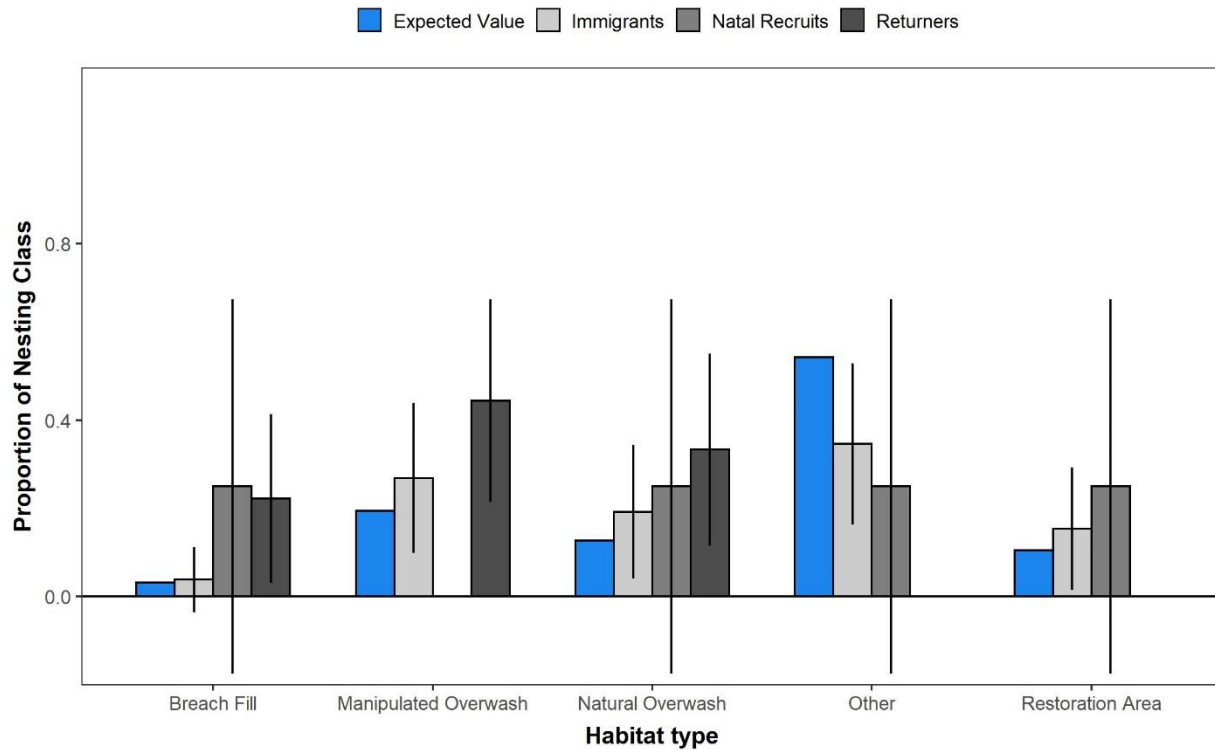


Figure A-3. Habitat used by immigrants, natal recruits, and returners in 2016 in relation to the expected usage based on availability of breach fill, manipulated overwash, natural overwash, other, and restoration area habitats. Error bars represent the 95% confidence intervals and selection is evident when error bars do not overlap the expected habitat use value. (Immigrants: $\chi^2 = 4.12$, $P = 0.39$, Natal Recruits: $\chi^2 = 8.74$, $P = 0.068$. Returners: $\chi^2 = 44.25$, $P < 0.001$.)

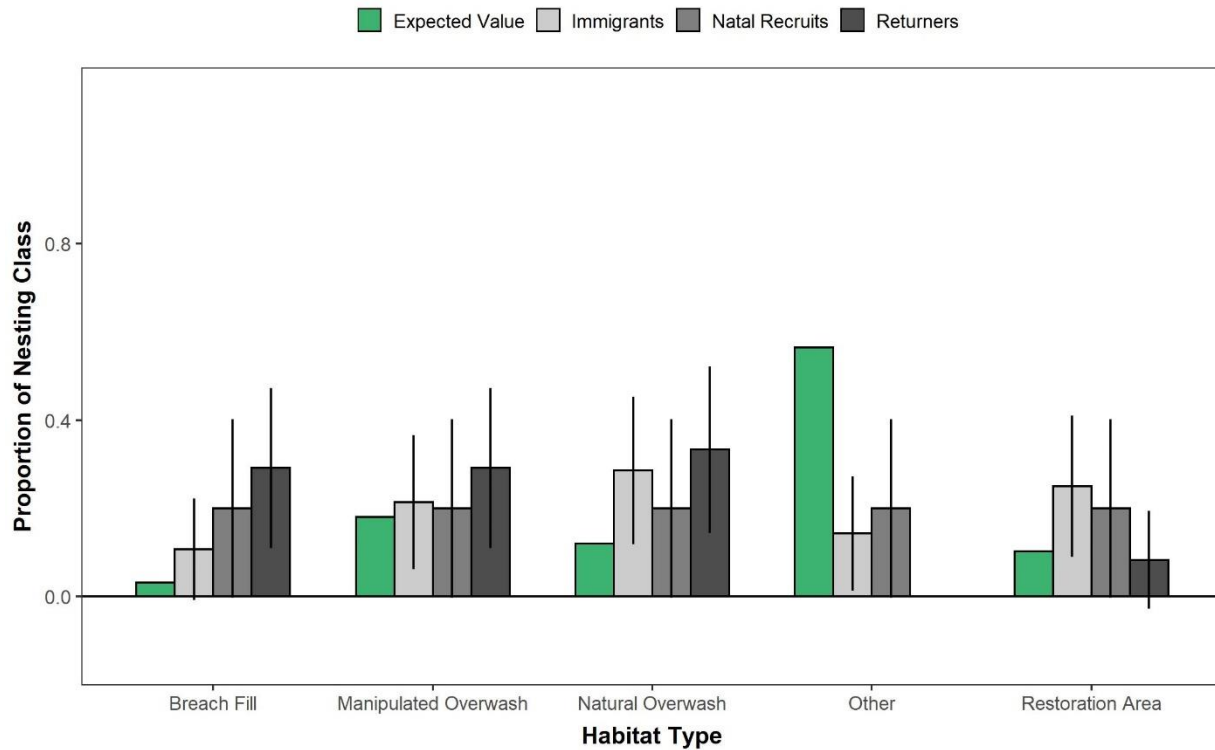


Figure A-4. Habitat used by immigrants, natal recruits, and returners in 2017 in relation to the expected usage based on availability of breach fill, manipulated overwash, natural overwash, other, and restoration area habitats. Error bars represent the 95% confidence intervals and selection is evident when error bars do not overlap the expected habitat use value. (Immigrants: $\chi^2 = 19.23$, $P < 0.001$. Natal Recruits: $\chi^2 = 19.23$, $P < 0.001$. Returners: $\chi^2 = 75.83$, $P < 0.001$.)

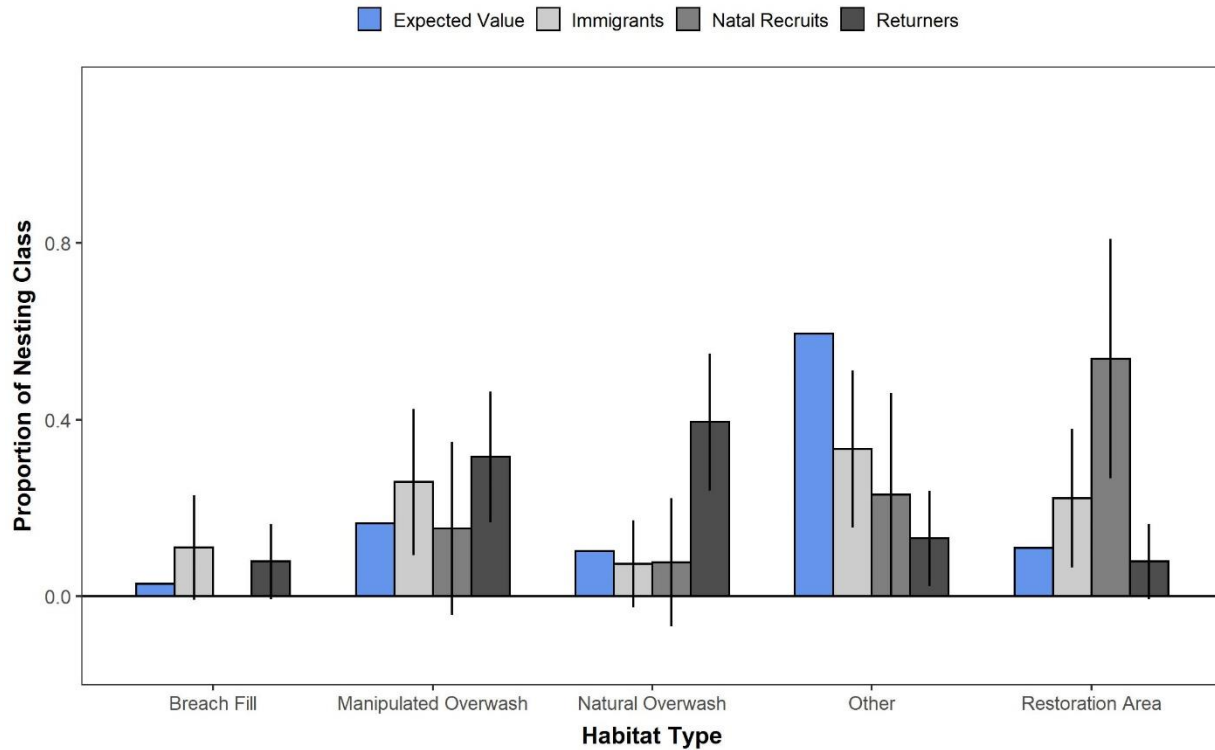


Figure A-5. Habitat used by immigrants, natal recruits, and returners in 2018 in relation to the expected usage based on availability of breach fill, manipulated overwash, natural overwash, other, and restoration area habitats. Error bars represent the 95% confidence intervals and selection is evident when error bars do not overlap the expected habitat use value. (Immigrants: $\chi^2 = 14.56$, $P = 0.006$. Natal Recruits: $\chi^2 = 25.11$, $P < 0.001$. Returners: $\chi^2 = 54.48$, $P < 0.001$.)

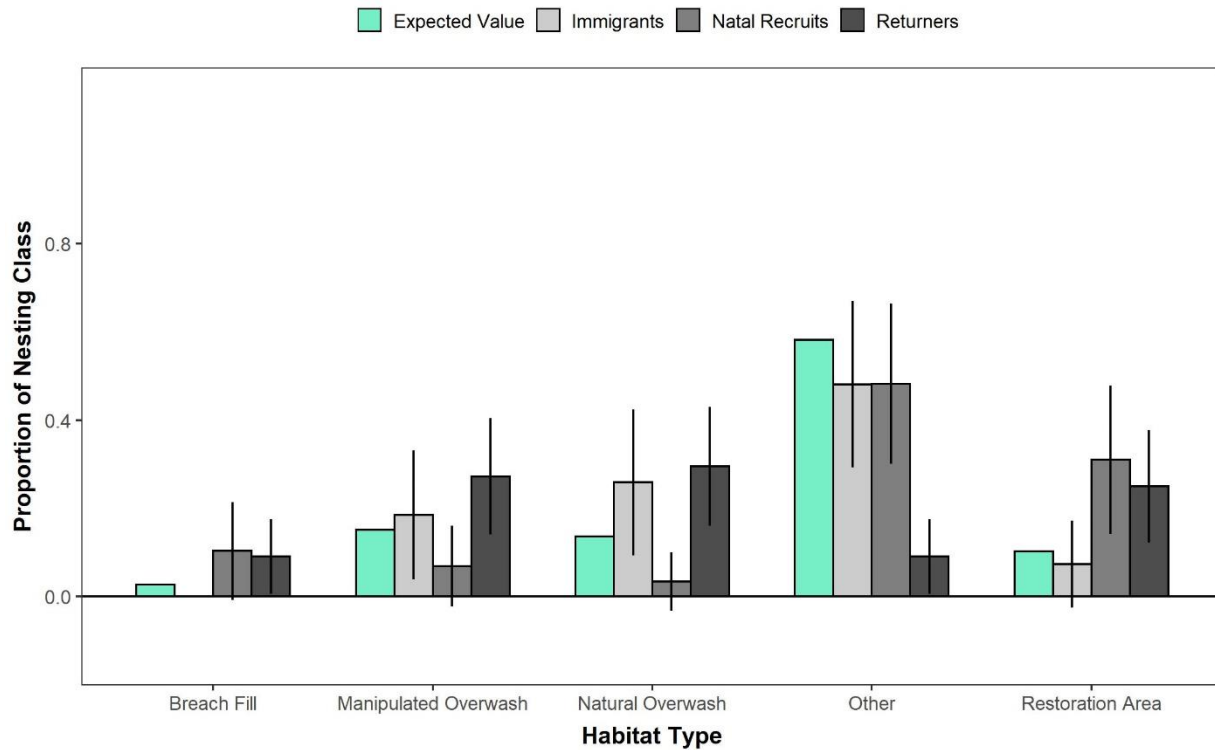


Figure A-6. Habitat used by immigrants, natal recruits, and returners in 2019 in relation to the expected usage based on availability of breach fill, manipulated overwash, natural overwash, other, and restoration area habitats. Error bars represent the 95% confidence intervals and selection is evident when error bars do not overlap the expected habitat use value. (Immigrants: $\chi^2 = 4.61$, $P = 0.33$. Natal Recruits: $\chi^2 = 22.35$, $P < 0.001$. Returners: $\chi^2 = 46.50$, $P < 0.001$.)

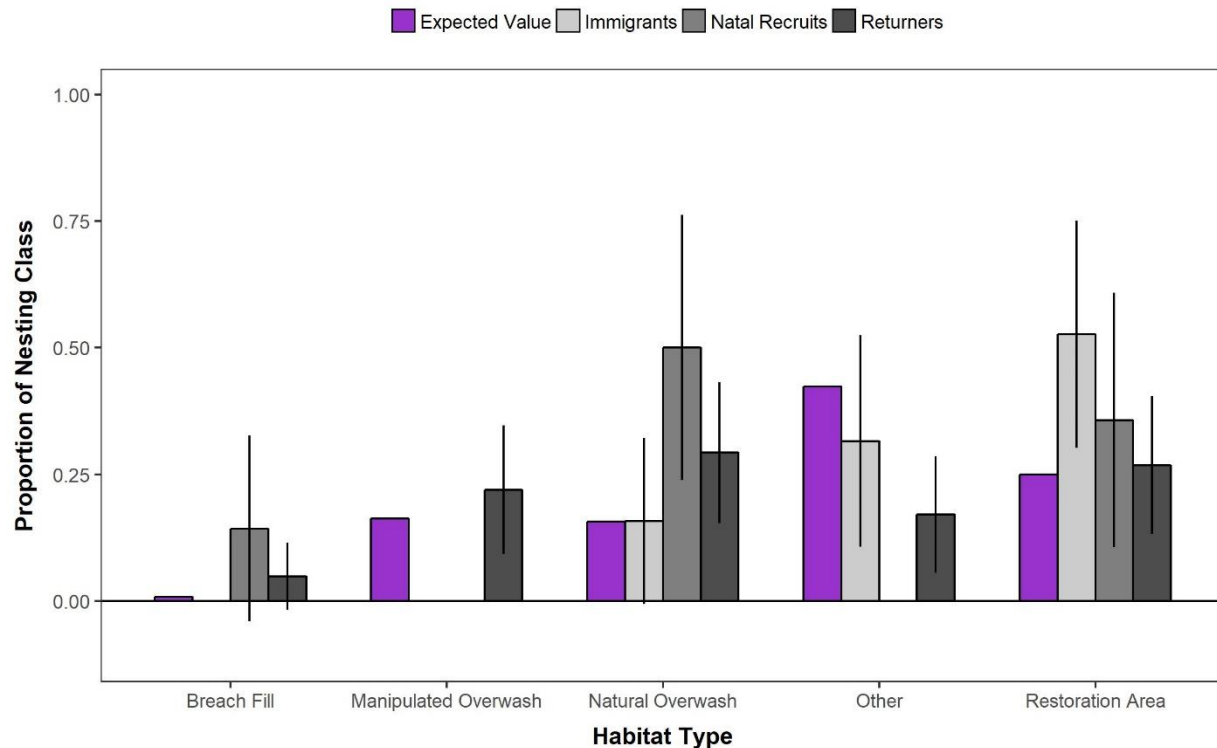


Figure A-7. Habitat used by immigrants, natal recruits, and returners in 2020 in relation to the expected usage based on availability of breach fill, manipulated overwash, natural overwash, other, and restoration area habitats. Error bars represent the 95% confidence intervals and selection is evident when error bars do not overlap the expected habitat use value. (Immigrants: $\chi^2 = 9.58$, $P = 0.05$. Natal Recruits: $\chi^2 = 52.06$, $P < 0.001$. Returners: $\chi^2 = 20.68$, $P < 0.001$.)