Red fox ecology and interactions with piping plovers on Fire Island, New York

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ACADEMIC ABSTRACT

Red foxes (*Vulpes vulpes*) have been identified as a key predator of the threatened piping plover (*Charadrius melodus*) along the U.S. Atlantic coast. However, little is known about coastal red fox ecology, making it difficult to create effective red fox management strategies in these settings. Here, we quantify aspects of red fox population, spatial, and dietary ecology and interactions with threatened piping plovers on Fire Island, New York.

We conducted remote camera surveys, scat and sign surveys, den monitoring, and GPS tracking of red foxes on the island in 2015–2018. We used these data to estimate red fox occupancy, reproduction, survival, and population density. We used GPS data to investigate red fox space use, habitat selection, and responses to piping plover nest exclosure setup, pre-hatch pipping, and hatching. We used fecal dietary analyses and data from den prey item surveys to quantify the frequency of piping plover predation and to identify major prey items of red foxes on the island.

Red fox occupancy remained high even after substantial decreases in abundance, population density, annual reproduction, and seasonal survival following 2 sarcoptic mange outbreaks. Within their home ranges, red foxes selected areas that were closer to vegetation during the daytime and twilight hours, but farther from vegetation at night. We did not find clear evidence that red foxes in our study area keyed in on piping plover nest exclosure setup, pipping, or hatching at the spatial scales considered in our comparisons, although fox penetration of and digging at exclosures was an issue in 2015 at Smith Point County Park. Items from Orders Rodentia (rodents, 43% of scats), Coleoptera (beetles, 38%), and Decapoda (crabs and other crustaceans, 29%) were most frequently found in 293 red fox scats examined. Skates (Family Rajidae, 89% of dens with food items) and Atlantic surf clams (*Spisula solidissima*, 67%) were found most frequently outside of dens. We did not find any identifiable piping plover remains in red fox scats or outside of dens.

Our results suggest that direct interactions between red foxes and piping plovers during our study period and in our study area were less frequent than expected, but concurrent work by collaborators documented that the trap success of red foxes was negatively related to piping plover reproductive output during our study period. Lethal removal of red foxes is unlikely to eliminate them from shorebird nesting areas unless complete eradication of foxes from the island can be achieved. We recommend strategic vegetation management in and around piping plover nesting areas to reduce daytime resting areas and hunting cover for red foxes, and continued use of nest exclosures. We also recommend further investigation into indirect impacts of red foxes on piping plover populations, and into the possibility that anthropogenic food resources could be subsidizing the island's red fox population.

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GENERAL AUDIENCE ABSTRACT

Red foxes have been identified as a key predator of the piping plover, a small migratory shorebird that breeds along the U.S. Atlantic coast and is considered ‘threatened’ (at risk of becoming endangered and eventually disappearing) within the United States. The lack of information about red fox ecology in coastal settings has been a challenge for wildlife biologists tasked with reducing predation on piping plovers. We investigated red fox ecology, behavior, and interactions with piping plovers on Fire Island, New York.

We used trail cameras, collected scat (feces), monitored dens, and tracked red foxes on the island with global positioning system (GPS) collars in 2015–2018. We used these data to estimate red fox distribution, litter sizes, survival rates, and population sizes. We used GPS data to estimate red fox territory sizes, describe habitat selection, and investigate responses to piping plover nest exclosure setup, pipping (a period before hatching during which chicks vocalize inside the eggs), and hatching. We dissected red fox scats and recorded prey items found outside of dens to determine what red foxes on the island were eating.

The proportion of each study area used by red foxes remained high even after substantial decreases in abundance, population density, annual reproduction, and seasonal survival following 2 parasitic disease (sarcoptic mange) outbreaks. Within their territories, red foxes selected areas that were closer to vegetation during the daytime and twilight hours but farther from vegetation at night. We did not find clear evidence that red foxes in our study area keyed in on piping plover nest exclosure setup, pipping, or hatching, although fox penetration of and digging at exclosures was an issue in some years at a site not included in those comparisons.

Rodents, beetles, and crustacean remains were found most frequently in red fox scats. Skates and surf clams were found most frequently outside of dens. We did not find any identifiable piping plover remains in red fox scats or outside of dens.

Our results suggest that that direct interactions between red foxes and piping plovers may be less frequent than previously believed, but concurrent work by collaborators documented that the trap success of red foxes was negatively related to piping plover reproductive output during our study period. Lethal removal of red foxes is unlikely to eliminate red foxes from shorebird nesting areas unless all foxes on the island are removed. We recommend strategic vegetation removal in and around piping plover nesting areas to reduce daytime resting spots and hunting cover for red foxes, and continued use of nest exclosures. We also recommend further investigation into indirect impacts of red foxes on piping plover populations, and into the possibility that anthropogenic food resources could be subsidizing the island's red fox population.

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I am especially grateful to my fellow graduate students on this project, Henrietta Bellman, Sam Robinson, and Katie Walker. Thank you for your camaraderie and support throughout this process, and for all that you have taught me about Fire Island’s avian and plant communities. I also want to extend a special thank you to my fellow officemates in Cheatham 124, Erin Heller, Earle Berge, Brandon Semel, Majango Wura, and Kayla Davis, for making my home away from home such a wonderful and welcoming space. I can’t thank you enough for all of the emotional support, humorous office chatter, puppy snuggles, and houseplants that you have shared with me. Thank you to all of my fellow Virginia Tech Shorebird Program folks as well, especially Don Fraser and Shannon Ritter, for all of your support and help with field logistics.

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ATTRIBUTIONS

This section describes the contributions made by coauthors towards each of the chapters included in this dissertation.

Chapter 1. Sarcoptic mange as a driver of red fox population dynamics in a coastal ecosystem

Sarah Karpanty and James Fraser (Department of Fish and Wildlife Conservation, Virginia Tech) secured funding, provided support, provided methodological and analytical guidance, and substantially edited the manuscript. Daniel Catlin (Department of Fish and Wildlife Conservation, Virginia Tech) secured funding and edited the manuscript. Benjamin Sacks (Veterinary Genetics Laboratory; University of California, Davis) oversaw all genetic analyses, assisted in interpreting genetic analysis results, and edited the manuscript.

Chapter 2. Red fox home range, activity patterns, and habitat selection on an Atlantic barrier island

Sarah Karpanty and James Fraser (Department of Fish and Wildlife Conservation, Virginia Tech) secured funding, provided support, provided methodological and analytical guidance, and substantially edited the manuscript. Shannon Ritter (Department of Fish and Wildlife Conservation, Virginia Tech) provided logistical support, conducted all landcover classification analyses, provided analytical guidance, and shared a variety of spatial data. Daniel Catlin (Department of Fish and Wildlife Conservation, Virginia Tech) secured funding, provided support, and edited the manuscript.

Chapter 3. Using GPS location data to assess potential red fox responses to predator exclosures at piping plover nests

Sarah Karpanty and James Fraser (Department of Fish and Wildlife Conservation, Virginia Tech) secured funding, provided support and methodological and analytical guidance, and substantially edited the manuscript. Samantha Robinson and Henrietta Bellman (Delaware Division of Fish and Wildlife) and Katie Walker (Department of Fish and Wildlife Conservation, Virginia Tech) assisted with data collection. Daniel Catlin (Department of Fish and Wildlife Conservation, Virginia Tech) secured funding, provided support, and edited the manuscript.

Chapter 4. Red fox dietary ecology in a semi-urban coastal ecosystem

Sarah Karpanty and James Fraser (Department of Fish and Wildlife Conservation, Virginia Tech) secured funding, provided support, and methodological and analytical guidance, and substantially edited the manuscript. Daniel Catlin (Department of Fish and Wildlife Conservation, Virginia Tech) secured funding and edited the manuscript. Benjamin Sacks (Veterinary Genetics Laboratory; University of California, Davis) oversaw all genetic analyses, assisted in interpreting genetic analysis results, and edited the manuscript.

INTRODUCTION

Barrier islands provide important habitat for many wildlife species, including nesting and migrating shorebirds (Erwin 1996, Gieder et al. 2014). These dynamic ecosystems are frequently impacted by hurricanes and storm events, and are vulnerable to sea-level rise (Gieder et al. 2014, Zeigler et al. 2019). Efforts to protect human lives and property from flooding and storm damage can result in significant modification of barrier island habitats through artificial dune construction, dune and beach renourishment, and the construction of shoreline stabilization structures (Houghton 2005, Peterson and Bishop 2005, Cohen et al. 2009, Charbonneau et al. 2016). Although these habitat modifications may aid in decreasing storm-related damage to human structures on the islands, they can also negatively affect wildlife species that rely on undisturbed coastal habitat, such as the federally threatened piping plover (*Charadrius melodus*), by inhibiting natural geomorphological processes (Elias et al. 2000, Houghton 2005, Cohen et al. 2009).

In October of 2012, Hurricane Sandy made landfall in the northeastern United States. The storm and associated storm surges damaged human structures along the U.S. Atlantic coast, particularly in New Jersey and New York, and led to many human deaths. The storm also resulted in dramatic changes in wildlife habitats in hard-hit coastal areas. Fire Island, New York, which is a barrier island along the south shore of Long Island, was breached in 3 places and overwashed in several others. The island’s dunes alsowere significantly eroded by the storm surge (Hapke et al. 2013).

As part of shoreline stabilization efforts in response to storm damage and public demand for protection against future storms, the U.S. Army Corps of Engineers requested a Biological Opinion from the U.S. Fish and Wildlife Service regarding potential effects of the Fire Island

Inlet to Moriches Inlet Coastal Storm Risk Reduction Project (FIMI) on piping plovers and other federally protected species in the project area. The resulting Biological Opinion included provisions for various habitat mitigation and monitoring activities, requiring that several monitoring priorities towards piping plover recovery on Fire Island be addressed in order for the proposed stabilization activities to continue. One of these priorities was in-depth predator monitoring to collect data that could be used towards the creation and implementation of a predator management plan to improve piping plover reproduction and survival on the island (USFWS 2014).

Red foxes have been a key predator of piping plovers on Fire Island (USFWS 2014), and in other barrier island ecosystems (Rimmer and Deblinger 1990, Patterson et al. 1991, Cohen et al. 2009, Gieder 2015). Patterson et al. (1991) identified red foxes as the most common cause of nest loss due to predation, responsible for 47.6% of predated nests, during their study of piping plover productivity on Assateague Island, Maryland and Virginia. Similarly, red foxes were the most common predator of unexclosed piping plover nests in studies conducted at Crane Beach, Massachusetts (Rimmer and Deblinger 1990) and West Hampton Dunes, New York (Cohen et al. 2009), comprising 44.4% and 50%, respectively, of predated nests for which the predator species could be identified. Additionally, Cohen et al. (2009) observed red foxes as the sole predator of exclosed nests during their study, in which 22.9% of exclosed nests were depredated by red foxes that learned to penetrate the exclosure. These findings suggest that the impacts of red foxes are an important factor to consider in planning for piping plover recovery, and that information on red fox ecology should be incorporated into predator management plans intended to benefit piping plovers.

Previous studies have examined red fox population, spatial, and dietary ecology in a variety of settings (*see* Lloyd 1980, Ables 1983, Henry 1986, Baker and Harris 2004, Soulsbury et al. 2010, *and others*). However, little information on red fox ecology on Fire Island or other barrier islands exists (USFWS 2014). Through my dissertation research, I aimed to address these gaps in scientific knowledge while collecting information on red fox ecology and interactions with piping plovers that could be used to guide future predator management activities intended to benefit piping plovers and sustain red fox populations, depending on the goals of managers.

We began collecting data on red foxes on Fire Island in 2015 as part of a larger project monitoring piping plovers and their response to shoreline stabilization activities on the island and on nearby Westhampton Island. The Virginia Tech Shorebird Program has been conducting in-depth monitoring of piping plovers and other shorebirds on Fire Island since 2013 in order to assess piping plover responses to Hurricane Sandy and associated shoreline stabilization and habitat restoration efforts (Walker et al. 2019, Weithman et al. 2019, Monk et al. 2020, Robinson at al. 2020). In addition, a detailed study of vegetation and habitat changes on the island was conducted in 2015–2017 (Bellman 2019). These concurrent studies have allowed for a rare side-by-side comparison of a predator population, a prey population, and the habitat in which these populations interact.

In Chapter 1, "Sarcoptic mange as a driver of red fox population dynamics in a coastal ecosystem," we describe the impacts of 2 sarcoptic mange outbreaks on the red fox population of Fire Island. Using a combination of remote camera surveys, GPS-collaring of red foxes, individual and den monitoring, and noninvasive genetic data, we estimated red fox occupancy, relative activity levels, annual reproduction, seasonal survival rates, relative abundance, and minimum population density at 3 study sites on the island. We then compared these population parameters before, during, and after the mange outbreaks.

In Chapter 2, “Red fox home range, activity patterns, and habitat selection on an Atlantic barrier island,” we used GPS collar data collected from red foxes to estimate home range and core use area sizes, describe daily activity patterns, and investigate within-home range habitat selection among red foxes on Fire Island, New York. We used generalized linear mixed modeling and resource selection functions to identify factors influencing each of these aspects of red fox ecology on the island, including the impacts of the 2 sarcoptic mange outbreaks during the study period.

In Chapter 3, “Using GPS location data to assess potential red fox responses to predator exclosures at piping plover nests,” we used location data from GPS-collared red foxes to examine the short-term spatial responses of red foxes to nest exclosure setup, pre-hatch pipping, and hatching at piping plover nests. We compared the distances from all recorded red fox locations to nests within their home range, and the proportion of red fox locations within a 100-m buffer of these nests, in the 48-hour periods before versus after exclosure setup, the start of pre-hatch pipping, and hatching. We also examined individual red fox responses to these events in more detail, conducting separate analyses of each fox’s location data before versus after events.

Finally, in Chapter 4, “Red fox dietary ecology in a semi-urban coastal ecosystem,” we used fecal diet analysis and den prey surveys to describe the diet of red foxes on Fire Island. We also compared encounter rates of anthropogenic foods at breeding dens, den proximity to development, and litter sizes to determine whether anthropogenic food resources might be subsidizing the island’s red fox population.

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CHAPTER 1.

Sarcoptic mange as a driver of red fox population dynamics in a coastal ecosystem

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Sarcoptic mange as a driver of red fox population dynamics in a coastal ecosystem

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ABSTRACT Sarcoptic mange has been identified as a driver of red fox (*Vulpes vulpes*) population dynamics in many parts of the world, but there is relatively little published information on its effects in North American red fox populations, particularly in coastal ecosystems. Here, we describe the impacts of two sarcoptic mange outbreaks on red fox population ecology at three study sites on Fire Island, New York. Using a combination of GPS-collars, remote camera surveys, den monitoring, and noninvasive genetic data, we estimated red fox trap success (remote camera detections/100 trap nights), occupancy, annual reproduction, survival rates, relative abundance, and minimum population density on the island before, during, and after mange outbreaks. Red fox trap success decreased by 85–100% following mange outbreaks at each site, but occupancy remained high (≥0.82) as long as foxes were present.

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Minimum known abundance and population density also decreased following mange outbreaks, with mean densities of 7.25 foxes/km^2 (SE = 1.85 foxes/km^2) before outbreaks, 2.74 foxes/km^2 (SE = 1.35 foxes/km^2) during outbreaks, and 0.17 foxes/km^2 (SE = 0.00 foxes/km^2) following outbreaks. Complete reproductive failure occurred following mange outbreaks at each site. Known survival rates of GPS-collared foxes during tracking periods ranged from 0.75–1 before the outbreaks, but only 0–0.38 during outbreaks. Thus, red fox occupancy remained high even after substantial decreases in relative abundance, population density, reproduction and survival. The outcomes of these mange outbreaks can be considered as a proxy for what may happen under intensive lethal removal of red foxes to manage predation of threatened and endangered shorebirds. Our findings suggest that while such efforts may reduce red fox abundance and population density within a given area, they may not be effective in reducing the spatial distribution of red foxes nor in eliminating the risk of predation from remaining foxes.

KEY WORDS barrier island, population dynamics, red fox, sarcoptic mange, *Sarcoptes scabiei, Vulpes vulpes*

Sarcoptic mange has been identified as a driver of red fox (*Vulpes vulpes*) 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, most of the published literature about mange in red foxes comes from European studies, and there is little information on the effects of sarcoptic mange in North American red fox populations (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 population 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 include red fox populations in coastal settings.

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 known to be key predators of piping plovers 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. 2019). Shortly after the initiation 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. 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 seasonal survival/mortality rates for red foxes on the island, and compared these population parameters before, during, and after mange outbreaks.

STUDY AREA

Fire Island is one of several barrier islands off the southern coast of Long Island, New York. It is approximately 50 km long, ranges from ~150–400 m wide, and currently is divided into two sections by Old Inlet, a historic inlet that was re-opened by Hurricane Sandy in October 2012. Measuring ~400 m across, this inlet appears to have prevented red fox movement between the 2 sections of the island during our study (*see Chapter 2*). Much of the island is managed as county, state, or national parks, with small villages and communities intermixed between Kismet and Watch Hill (Fig. 1). In addition to red foxes, domestic cats (*Felis catus*), domestic dogs (*Canis lupus familiaris*), and raccoons (*Procyon lotor*) were present and widespread within the study area. Opossums (*Didelphis virginiana*), American mink (*Neovison vison*), and long-tailed weasels (*Mustela frenata*) were present in some areas, but were relatively uncommon during the study (K.M. Black, Virginia Tech, unpublished data). While GPS-collared red foxes traveled throughout Fire Island during this study, our research efforts were focused at 3 sites: 1) Robert Moses State Park and the Fire Island National Seashore Lighthouse Tract, 2) the portion of the Fire Island National Seashore Otis Pike High Dune Wilderness Area that lies west of Old Inlet (hereafter referred to as the "Western Wilderness"), and 3) Smith Point County Park and the portion of the Fire Island National Seashore Otis Pike High Dune Wilderness Area that lies east of Old Inlet (hereafter referred to as "Old Inlet East"; Fig. 1).

Habitat types on the island included ocean beach, dune and interdune areas, shrub/scrub, evergreen and maritime forest, and bayside flat, beach and marsh (Fig. 2). In addition, many portions of the island were developed for recreation and/or residential use. These developments included several designated off-road vehicle recreation areas within the state and county parks. Causeways near the west and east ends of the island provided driving access between Long Island, New York, and Fire Island, New York, with short sections of paved roadway providing driving access between the causeways and major recreation areas. Most other roads on the island were unpaved, with vehicle traffic strictly limited and subject to seasonal and episodic closures. While we did not observe any red foxes or other wildlife successfully using the western causeway to travel on or off the island, we received reports and a photograph of one red fox doing so across the much shorter eastern causeway (photograph shared on 17 January 2019; S. Papa, U.S. Fish and Wildlife Service, personal communication).

METHODS

Field methods

Fox capture, ear tagging, and GPS collaring

During August–December 2015, April–May 2016, and February–April 2017 and 2018, we captured a portion of the red fox population in each study site using padded and offset-jaw 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, USA) 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, USA) 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. In contrast, the small metal ear tags were not intended to be visible in remote camera photos or during transect surveys, but were meant only to assist in identifying any individuals recaptured in future years.

Following the detection of mange at study sites, we took precautionary steps to minimize the risk of spreading the disease among the population and between sites during trapping activities. These precautions included wearing sanitized rubber gloves and disposable Tyvek suits when handling trapped foxes; sanitizing all capture and measurement equipment in between uses with disinfecting wipes, disinfecting spray, or machine washing with borax and machine drying on the highest temperature setting; and removing traps that captured a fox from the rotation of use for the rest of that season's trapping period.

GPS tracking

We also outfitted a sample of red foxes in each site with GPS collars. The GPS collars (Quantum 4000E, medium size; Telemetry Solutions, Concord, CA, USA) included a VHF transmitter and 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 relocations, we also checked for mortality signals, and used VHF signals to locate the remains of red foxes that had died. We attempted to determine a cause of death through close inspection of fox 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. 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 ~300 m from each other following a general north-south direction across the island (Fig. 2). These transects ran from the ocean high tide line through all passable habitats to the bayside high tide line, or the point where bayside transects became impassable 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).

During 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 for all red foxes encountered during surveys. We collected, in separate paper bags, each potential red fox scat found that appeared to be ≤1 month old, based on visible degradation of fecal material. We recorded the age (adult or kit), and ear tag color and number (if one was visible) for all red foxes encountered during surveys. At 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 of den entrances, 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 game trails and transect areas typically surveyed during other months.

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 (Fig. 1). During these surveys, we recorded GPS locations for 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, USA) aimed at den entrances and/or adjacent clearings. 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 established an unbaited camera station within 50 m of the center point of each grid cell containing suitable locations. 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, USA), 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 (Appendix A, Fig. A1). 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 freezer for storage until DNA subsampling. For each sample, we separated a small portion (approximately 2 ml) 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, Sacks et al. 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, 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 unidentifiable red fox photographed within 30 minutes of a previous series of unidentifiable 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, 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 red foxes at a given site; "during outbreak," if signs of mange were 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 foxes) 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, MacKenzie et al. 2006). We used a single species, single season framework in Program PRESENCE (Version 2.12.21, https://www.mbr-pwrc.usgs.gov/software/presence.html, accessed 12 September 2016). We did not collapse data, but rather each day was considered an encounter occasion. Thus, our estimated occupancy relates to the entire survey period, while detection rates are interpreted as daily detection probabilities. 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 used a threshold of 4 ΔAIC 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 10 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 conservative estimates, as we could not determine whether some breeding dens belonged to a known breeding group, versus an additional, previously uncounted breeding group. We used a Kruskal-Wallis test to compare litter sizes before, 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, defined as the proportion of GPS-collared foxes that survived through the end of the planned tracking period. We used Pearson's chi-square tests for equal proportions to test whether survival differed before, 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, 10 August 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 each year from 1 February–10 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–10 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 included red foxes that were observed during this census period 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 that were hand-delineated based on aerial imagery (flown in April 2016) and the "Calculate Geometry" tool in ArcMap 10.6 (ESRI, Redlands, CA, USA). We used a Kruskal-Wallis test to compare minimum red fox density before, 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 it was first documented in a photograph taken by a visitor at Smith Point County Park which 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 (Appendix A, Table A1), based on widespread hair loss, facial crusting, and skin lesions visible in the photograph. These symptoms have been used to successfully identify cases of moderate and severe mange in photographed animals in previous studies, but may be insufficient to detect mild cases (Brewster et al. 2017, Carricondo-Sanchez et al. 2017, Niedringhaus et al. 2019). For the purposes of our analyses, we conservatively only identified animals with extensive hair loss, multiple skin lesions, and/or facial crusting as likely being affected by mange. Prior to fall of 2015, we had not observed any red foxes with hair loss, facial crusting, multiple 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, Virginia Tech Shorebird Program, 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 we outfitted 33 of these red foxes with GPS collars (Table 1), 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 foxes 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.

Trap success and occupancy

Red fox trap success during remote camera surveys varied among periods (before, during, and after the mange outbreaks, Fig. 3, Kruskal-Wallis test, χ_2^2 = 8.43, *P* = 0.01). 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 as the outbreak there was ongoing, decreased by 100% the following year, and remained low through the end of the study. At Robert Moses State Park, red fox trap success decreased by 85% following the beginning of the mange outbreak at that site (119.95 red fox detections/100 trap nights in 2016, 18.36 red fox detections/100 trap nights in 2017). In the Western Wilderness, red fox trap success decreased somewhat following the beginning of the mange outbreak at that site, but it was not until the following year that we observed a 92% decrease in trap success compared to pre-mange levels (103.36 red fox detections/100 trap nights in 2016, 8.30 red fox detections/100 trap nights in 2018; Fig. 3).

Top occupancy models differed across sites and years in whether detection probability was best modeled as constant or varying by day (Table 2). 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 3, Fig. 4). 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 3, Fig. 4). 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, 1.0 (Table 3, Fig. 4). This same pattern was observed in the Western Wilderness, where occupancy was 1.0 in 2015 and 2016, and in 2017 as the mange outbreak at this site was beginning. Occupancy in the Western Wilderness decreased to 0.86 in 2018, when the outbreak was still ongoing, but 95% confidence intervals still included 1.0 (Table 3, Fig. 4). Detection probabilities in all study sites varied, but generally declined during and after the mange outbreaks (Table 3).

Reproduction

We observed pronounced decreases in reproduction in the breeding seasons following the detection of mange at each site (Table 4). 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 groups stayed constant between 2016 and 2017, average litter size decreased by 20% compared to the 2016 average (2016: $\bar{x}$ = 3.5 kits/group, SE = 0.5 kits/group, n = 4 groups; 2017: $\bar{x}$ = 2.8 kits/group, SE = 0.5 kits/group, n = 4 groups). In 2018, there was 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 (2016: $\bar{x}$ = 3.6 kits/group, SE = 0.9 kits/group, n = 5 groups; 2017: $\bar{x}$ = 1 kits/group, SE = 0 kits/group, n = 2 groups). 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 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% at sites during and following the outbreaks (Table 5). 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 at those two sites.

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 dead of a suspected vehicle collision along an ORV road by project collaborators. Four red foxes were removed from the study area by humans during the data collection period, and were not included in our analyses (taken to a local wildlife rehabilitator for treatment of mange/other injuries, n = 3; removed by U.S. Department of Agriculture’s Animal and Plant Health Inspection Service [USDA-APHIS] Wildlife Services, n = 1).

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: 1 red fox[died during the census period], 0.17 foxes/km^2, 5.94 km^2 total site area, Table 6, Fig. 5) and remained low throughout the rest of our study (2017 and 2018: 1 red fox, 0.17 foxes/km^2). 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/km^2, 4.63 km^2 total site area), and had decreased substantially by the 2018 census period (2018: 5 red foxes, 1.08 foxes/km^2). 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/km^2, 3.85 km^2 total site area), but decreased substantially afterwards (2018: 1 red fox, 0.26 foxes/km^2). Minimum red fox density differed before, during, and after mange outbreaks across sites (Kruskal-Wallis test, χ^2_2 = 6.16, $P \leq 0.05$), with higher densities observed before versus after outbreaks (post-hoc Dunn test, $Z = -2.43$, $P < 0.01$).

We collected and sent 268 potential red fox scat samples to the MECU for genetic analyses. Seventy-one 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 during years following the mange outbreaks, with 32 genotypes identified in samples from 2016 (prior to the outbreak west of Old Inlet, n = 130 scats and 4 tissue samples) and 12 identified in samples from 2017 (n = 100 scats and 2 tissue samples) and

14 genotypes identified in samples from 2018–February 2019 (n = 38 scats and 1 tissue sample). 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.

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 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 (Appendix A, Table A2), 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.

DISCUSSION

Our combined observations from monitoring GPS-collared and ear-tagged foxes, transect surveys, den monitoring, remote camera surveys, and genetic analysis of scats 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 (Lindström 1991, 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. 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 ± 0.04 SE. O'Connell et al. (2006) also reported lower red fox occupancy estimates on Cape Cod, MA (0.35 ± 0.17 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). In addition, estimated home range sizes from GPS-collared red foxes (*Chapter 3*) suggest that we likely had >1 camera station set up within each red fox territory, potentially violating the assumption that detection probabilities at camera stations were independent of each other. Thus, the occupancy estimates presented here are more accurately described as occurrence, rather than true occupancy.

With the exception of the ~1-year period where red foxes apparently were absent east of Old Inlet, our occupancy estimates across all sites and years were all ≥0.80, with confidence intervals up to or approaching 1, even in 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 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). The lack of significant changes in red fox occupancy despite significant changes in red fox abundance and population density suggests that occupancy may not have been informative as an index of red fox abundance in this study during our study period. We recommend further research into how red fox trap success and other indices of red fox abundance directly relate to shorebird predation risk, as these measures may be more informative for managers. In work conducted concurrently with this fox monitoring, we found evidence that red fox trap success was correlated with piping plover population metrics; piping plover chick survival in the study area was higher following mange outbreaks, when red fox trap success was lower (Robinson 2020).

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 spatial distribution of foxes or creating areas free of foxes unless complete eradication is 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 lead to increased occupancy via colonization of previously unoccupied sites and/or compensatory reproduction. 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) found no effect of lethal control on the relative abundance (based on spotlight surveys) of red foxes on sheep farms in southeast Australia, and hypothesized that rapid immigration of foxes following removal may occurred. Baker et al. (2006) similarly found that over-winter culling of red foxes in Wales, UK, did not significantly reduce the relative abundance (based on fecal density) of red foxes in commercial forests, presumably due to immigration of foxes from nearby areas. Harding et al. (2001) found that annual removal of an estimated 50% or more of the red fox population in their California study area was correlated with short-term decreases in red fox abundance, but high immigration rates appeared to be sustaining the population long-term.

Increased reproduction among remaining individuals may also compensate for the loss of removed individuals. For example, Marlow et al. (2016) observed 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 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 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 still are 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

These results demonstrate that red fox occupancy may remain high even after substantial decreases in abundance and population density following mange outbreaks. When the outcomes of these mange outbreaks are considered as a proxy for the potential outcome of 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.

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TABLES

Table 1. 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 foxes after collar deployment) are not included in this table. ♂ = male, ♀= female.

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

Table 2. 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. ΔAIC = difference in AIC value between candidate model and top-ranked model.

Site	Model[a]	AIC	ΔAIC	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	$\psi(.)\ p(.)$	968.62	0.00	1.0	1.0	2
	$\psi(.)\ p(\text{day})^b$					
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 3. 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

Table 4. 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 10 August of each year as a cutoff.

		2016		2017		2018	
Site	Mange first detected	Breeding groups	Mean kits/group (SE)	Breeding groups	Mean kits/group (SE)	Breeding groups	Mean 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

[a] Mange first detected at the site

[b] During mange outbreak at that site

[c] After mange outbreak at that site

Table 5. 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.

		2015		2016		2017		2018	
Site	Mange first detected	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

[a] During mange outbreak at that site

[b] One 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

Table 6. 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–10 August). We then estimated minimum red fox density by dividing the minimum red fox abundance by the area of each site (4.63 km^2 for Robert Moses State Park + Lighthouse Tract, 3.85 km^2 for the Western Wilderness, and 5.94 km^2 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 State Park + Lighthouse Tract	2016	6	0	5	14	0	25	5.40
	2017	8	2	5	13	1	29[a]	6.26
	2018	2	1	1	0	1	5[b]	1.08
Western Wilderness	2016	5	1	11	18	0	35	9.09
	2017	4	3	4	2	0	13[c]	3.38
	2018	0	0	0	0	1	1	0.26
Smith Point County Park + Old Inlet East	2016	1	0	0	0	0	1[d]	0.17
	2017	0	0	0	0	1	1	0.17
	2018	0	0	0	0	1	1	0.17

[a] 5 adults and 2 kits included in this count died during the census period

[b] 2 adults included in this count died during the census period

[c] 1 adult included in this count died during the census period

[d] 1 adult included in this count died during the census period

FIGURES

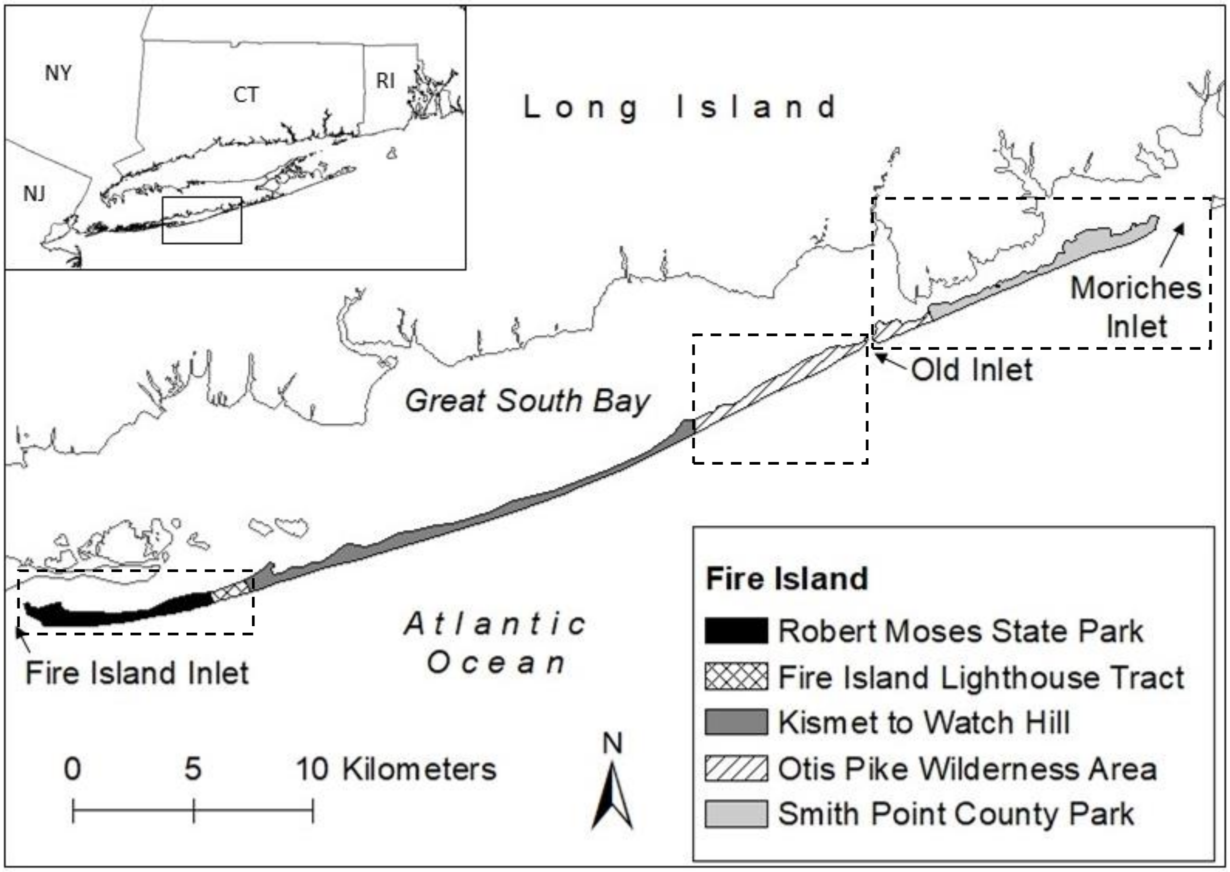


Figure 1. Map of study area on Fire Island, New York. Research efforts in 2015–2019 were focused at 3 sites, outlined in dashed boxes: 1) Robert Moses State Park and the Fire Island National Seashore Lighthouse Tract, 2) the portion of the Fire Island National Seashore Otis Pike High Dune Wilderness Area that lies west of Old Inlet (“Western Wilderness”), and 3) Smith Point County Park and the portion of the Fire Island National Seashore Otis Pike High Dune Wilderness Area that lies east of Old Inlet (“Old Inlet East”).

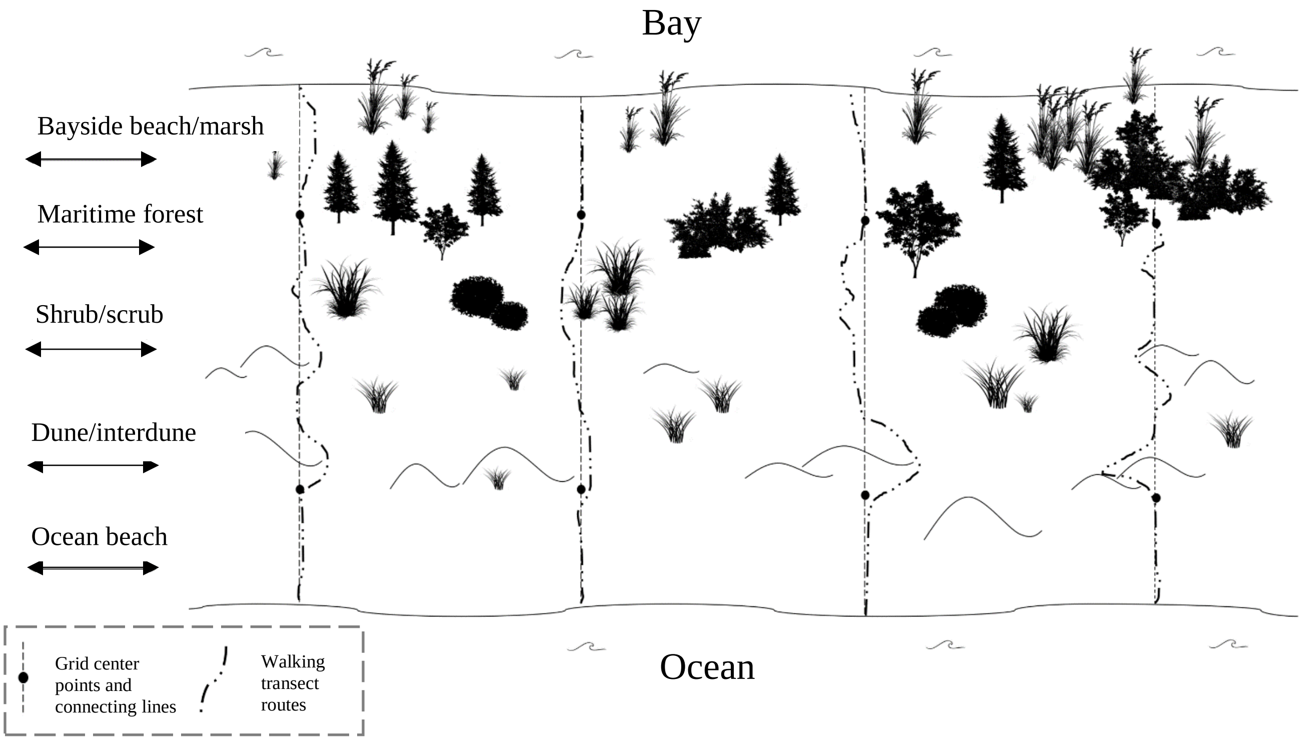


Figure 2. Diagram illustrating habitat types and transect surveys conducted on Fire Island, New York in 2016–2019. We followed game trails, edges, and other likely wildlife travelways along general north-south transect lines based on a 300-m grid overlay of the island. These transects spanned all passable habitat types within each 300-m section of the study area.

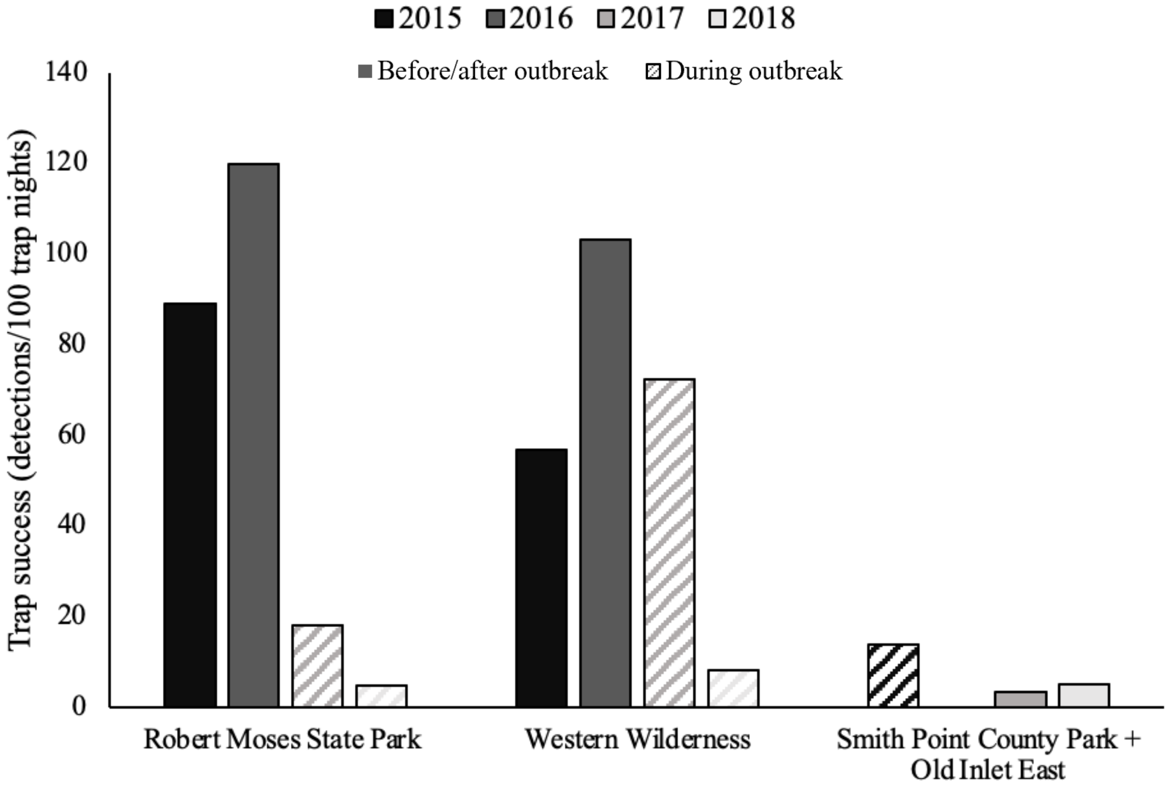


Figure 3. Red fox trap success (detections/100 trap nights) by site during each remote camera survey period on Fire Island, New York in 2015–2019. Remote camera surveys were conducted in September–February of each year, ending in February 2019. Solid bars indicate survey periods before or after mange 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.

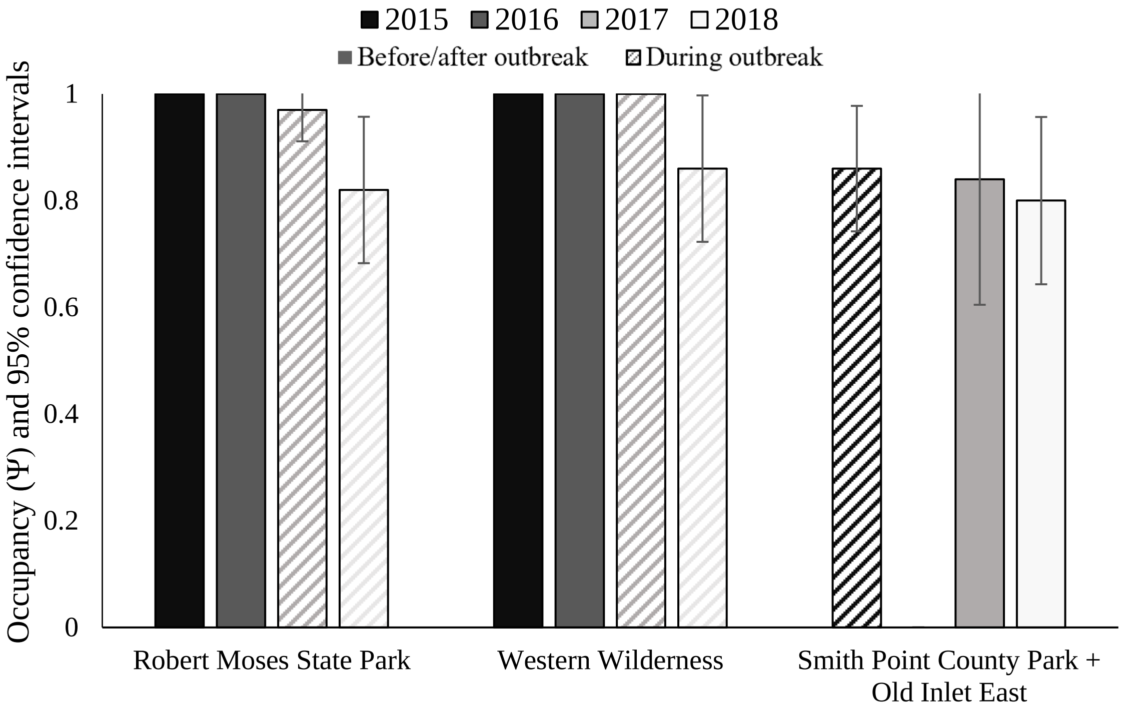
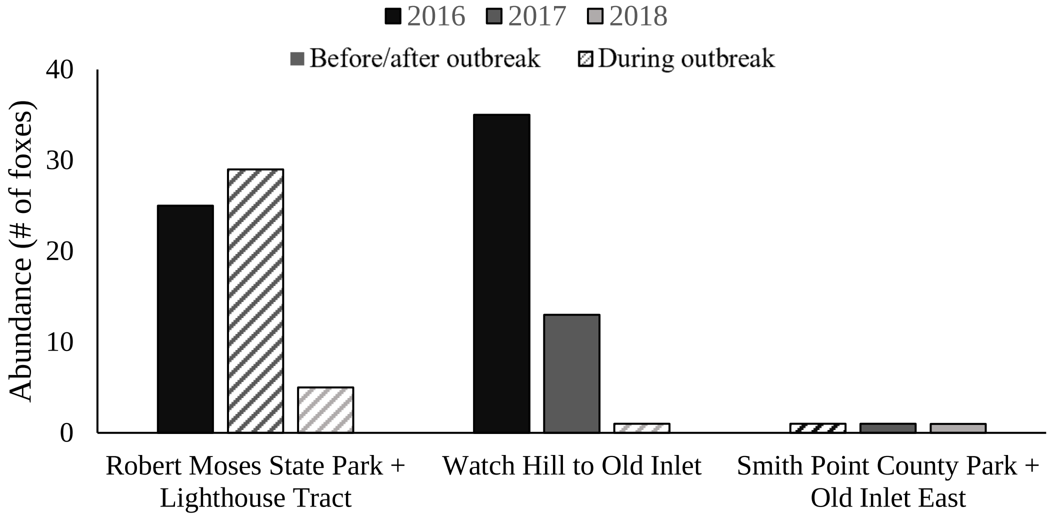


Figure 4. Red fox occupancy estimates and 95% confidence intervals by site during each remote camera survey period on Fire Isl ■ Before/after outbreak ▨ During outbreak ote camera surveys were conducted in September–February of each year, ending in February 2019. Solid bars indicate survey periods before 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.



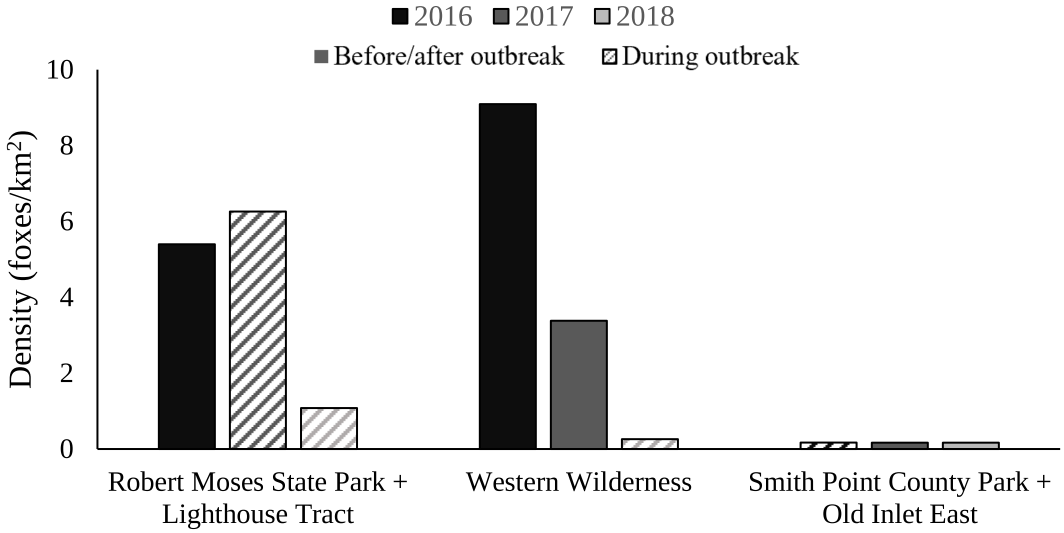


Figure 5. Minimum estimated red fox abundance (top) and density (bottom) by site in February–August of 2016–2018 on Fire Island, New York. Solid bars indicate census periods before or after mange outbreaks at each site, and hashed bars indicate census periods during mange outbreaks. No red foxes were detected at Smith Point County Park + Old Inlet East during the 2016 census period.

APPENDIX A: Supporting Information for Chapter 1

Table A1. 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. These symptoms have been used to successfully identify cases of moderate and severe mange in photographed animals in previous studies, but may be insufficient to detect mild cases (Brewster et al. 2017, Carricondo-Sanchez et al. 2017, Niedringhaus et al. 2019). For the purposes of our analyses, we conservatively only identified animals with extensive hair loss, multiple skin lesions, and/or skin crusting as likely being affected by mange.

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 may result 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 usually results in a "whip-like" appearance.

Table A2. 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	Western Wilderness	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.

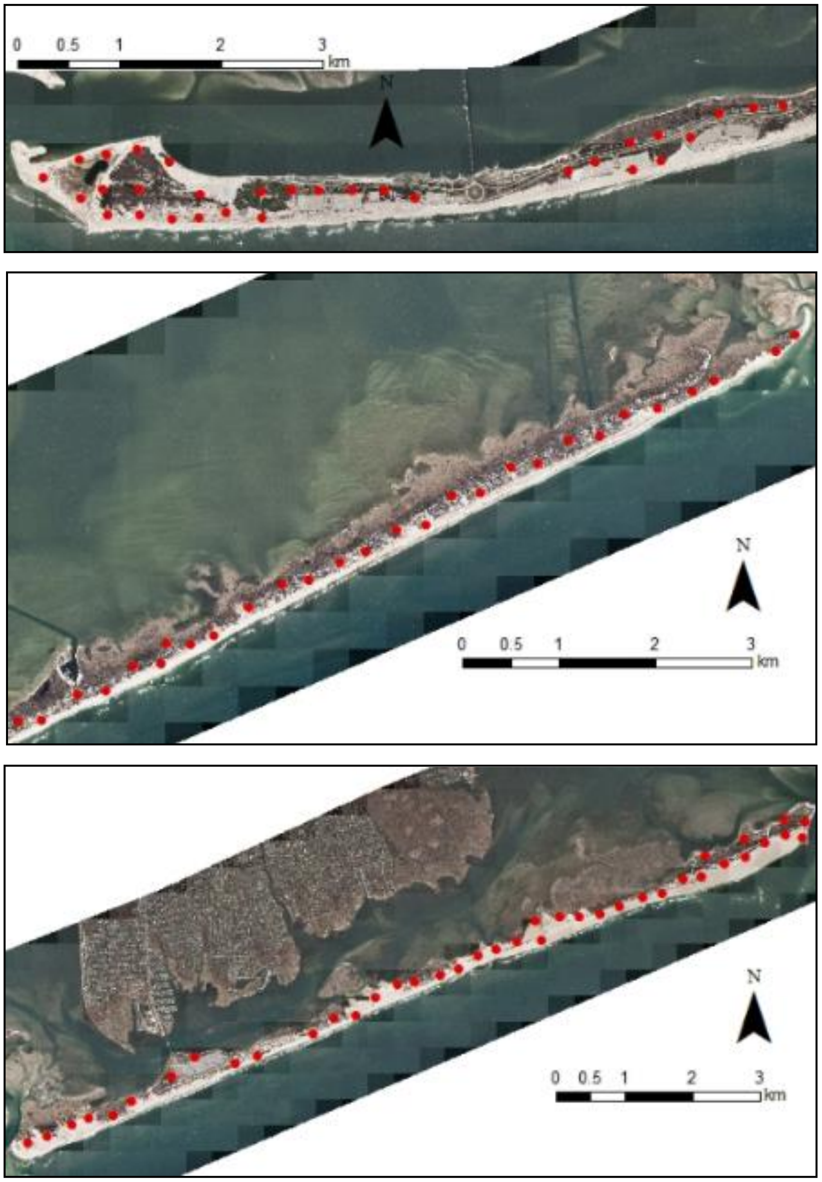


Figure A1. Approximate camera station locations (red dots) at Robert Moses State Park (top), in the Western Wilderness (middle), and Smith Point County Park + Old Inlet East (bottom) on Fire Island, New York in 2015–2019. Remote camera surveys were conducted in September–February of each year, ending 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.

CHAPTER 2.

Red Fox Home Range, Activity Patterns, and Habitat Selection on an Atlantic Barrier Island

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Red Fox Home Range, Activity Patterns, and Habitat Selection on an Atlantic Barrier Island

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ABSTRACT Red fox (*Vulpes vulpes*) spatial ecology has been described in a variety of geographic locations and habitats, but relatively little is known about red fox spatial ecology on barrier islands, where semi-linear habitat distribution and aquatic barriers may affect terrestrial movements. Because red foxes often are an important predator of imperiled shorebirds in these ecosystems, this information is needed to inform effective predator management. We used GPS collar data collected in 2015–2018 from 31 red foxes to estimate home range and core use area sizes, describe daily activity patterns, and investigate within home-range habitat selection among red foxes on Fire Island, New York. GPS-collared red fox home range sizes (95% time local convex hull [t-LoCoH] isopleths) averaged 164.44 ha ± 33.1 ha (SE), but varied widely with season and sex, ranging from 10.09 ha to 658.55 ha. Core use area sizes (50% t-LoCoH isopleths) averaged 25.68 ha ± 8.51 ha (SE) and varied with sex and sarcoptic mange infection status. Twenty-two of 31 red foxes maintained distinct home ranges throughout the monitoring period, while 9 were transient, regularly traveling through the home ranges of other red foxes and among management units across the island. Hourly movement rates varied across the diel cycle and individuals, averaging 216.33 m/hr ± 8.71 m/hr (SE), and were highest between 13 and 22 hours after sunrise. Within-home range habitat selection varied between diel activity periods; for example, red foxes selected areas closer to vegetation than expected based on habitat

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availability during the daytime and twilight hours, but farther from vegetation than expected at night. We recommend vegetation management in and around shorebird nesting areas to reduce daytime resting sites and hunting cover for red foxes while improving suitability for use by nesting shorebirds. When management units are small enough that red foxes can move among units, as observed in this study, predator management should be coordinated across management units.

KEY WORDS barrier island, habitat selection, home range, red fox, spatial ecology, *Vulpes vulpes*

The red fox (*Vulpes vulpes*) has the largest geographic distribution of all terrestrial carnivores, and it inhabits a wide variety of environments (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 several different 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 (Cohen et al. 2009, USFWS 2014, Gieder 2015, Hunt et al. 2019). Information on red fox home range size, activity patterns, and habitat selection in coastal ecosystems can be used to predict relative predation risk to shorebirds over space and time and inform decisions about the spatial scale of management activities.

Previous studies of red fox spatial ecology in coastal settings, including barrier islands and mainland coastal areas, 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. It is unknown how the unique geomorphology of barrier islands may impact these components of red fox spatial ecology, and the extent to which 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 long and narrow landforms with generally linear distribution of different habitat types running parallel to the ocean. 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 the space use, activity patterns, and habitat selection of red foxes on the island. Ultimately, we seek to use this knowledge of spatial ecology and habitat selection to inform predation management actions intended to benefit ground-nesting shorebird species, such as the piping plover.

STUDY AREA

Fire Island is one of several barrier islands along the southern coast of Long Island, New York. It is ~50 km long and ~150–400 m wide. It was separated into two portions by Old Inlet, a historic inlet which reopened during Hurricane Sandy in 2012 and remained open throughout this study, preventing terrestrial movement between the two sections. Habitat types on the island included ocean beach, dune, shrub/scrub, maritime forest, marsh, and developed areas (Bellman 2018, Walker et al. 2019). In addition to red foxes, domestic cats (*Felis catus*), domestic dogs (*Canis lupus familiaris*), and raccoons (*Procyon lotor*) were widespread within the study area. Opossums (*Didelphis virginiana*), American mink (*Neovison vison*) and long-tailed weasels (*Mustela frenata*) were present in some parts of the island, but were relatively uncommon during the study (K.M. Black, Virginia Tech, unpublished data). Many parts of the island have been intensively engineered through various beach scraping and renourishment projects (NPS 2008, Lentz and Hapke 2011, Kratzmann and Hapke 2012). Most of the island is managed as part of county, state, or national parks, while small villages and communities occupy the remaining areas. The island receives an estimated 2–3 million visitors per year, primarily during the June–August tourist season (NPS 2017). Causeways near the western and eastern ends of the island and short paved roadways provide driving access between Long Island and some park areas. With the exception of the causeways and designated off-road vehicle recreation areas, vehicle traffic on the island’s roads and outer beach was limited to residents, contractors, and public service providers, and subject to seasonal closures to protect nesting shorebirds.

As part of beach stabilization activities following Hurricane Sandy in 2012, the U.S. Army Corps of Engineers created 2 restoration areas, completed in 2015, which were intended to mitigate the effects of nesting habitat loss for piping plovers. These restoration areas, New Made (6.6 ha) and Great Gun (34.8 ha), were both created east of Old Inlet, within the borders of Smith Point County Park (USACE 2014, USFWS 2014, Walker et al. 2019).

Our research was focused in 3 geographic areas on Fire Island: 1) Robert Moses State Park and the Fire Island National Seashore Lighthouse Tract, 2) Fire Island National Seashore Otis Pike High Dune Wilderness Area (west of Old Inlet), and 3) Smith Point County Park and Fire Island National Seashore Otis Pike High Dune Wilderness Area (east of Old Inlet, Fig. 1).

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 minimize the chance of capturing non-target species. Upon capture, we manually restrained foxes, determined their sex and breeding status, and assessed their general physical condition. 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 later observed in the field and/or recaptured.

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 other 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 10–200 m 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).

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 estimate the latitude, longitude, and approximate altitude of a given location (Telemetry Solutions 2011). We conservatively excluded locations >10 m into the ocean surrounding the island, or with recorded elevation values >50 m (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 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. We conducted a cluster analysis to sort red foxes into 2 groups to identify 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 related to home range extent and consistency of space use.

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 several covariates on home range and core use area sizes of both resident and transient foxes, selecting the best model as described above.

Initial 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), sex, and breeding status (associated with an active breeding den 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 (*Chapter 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. Shortly after the initiation of data collection, a series of sarcoptic mange outbreaks began in the study area (*Chapter 1*, Robertson et al. 2019). We included mange status in our analyses as a binary variable reflecting whether or not an individual was affected by 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, based on the lowest AIC_c value. 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, Arnold 2010).

Activity patterns and modeling

We estimated hourly movement rates 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 fox 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, mange 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, selecting the best model as described above. 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 Millspaugh 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 [*Ammophila breviligulata*], 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 10.6 (ESRI 2018, Redlands, CA) 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.

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 followed the same steps described above to test for independence between covariates and to evaluate and compare models, and used k-fold cross-validation to assess the predictive power of the top supported model (Boyce et al. 2002).

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 (Appendix B, Table B1). 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 B1). 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.

Sarcoptic Mange Outbreaks

The first sarcoptic mange outbreak during the study 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 (*Chapter 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 (*Chapter 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 to 658.55 ha ($\bar{x}$ = 164.44 ha, SE = 33.31 ha, n = 33; Fig. 2). Core use (50% isopleths) area sizes also varied widely among individuals, ranging from 0.38 ha to 267.79 ha ($\bar{x}$ = 25.68 ha, SE = 8.51 ha, n = 33; Fig. 2).

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 nor with each other (correlation coefficients between all other metrics were >0.75). Based on cluster analysis results, red foxes that maintained relatively small home ranges (10-165 ha) were classified as residents (n = 22 red foxes, n = 24 data sets as two foxes were tracked during 2 tracking periods), while red foxes that maintained relatively large home ranges (245-659 ha) were classified as transients (n = 9; Fig. 3). 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 1). Home ranges were smaller in the spring/summer monitoring periods ($\bar{x}$ = 115.30 ha, SE = 34.12 ha, n = 23; β = -0.50 ± 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 areas were also smaller in the spring/summer monitoring periods ($\bar{x}$ = 20.17 ha, SE = 8.76 ha, n = 23; β = -0.33 ± 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 ± 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 1), 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 1), but did not show significant directional trends (breeding status β = -0.34 ± 0.34 SE, sex β = 0.24 ± 0.26 SE).

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 (Appendix B, Table B2). 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).

Hours since sunrise, residency, and mange status most strongly influenced hourly movement rates (Table 2). Mean observed hourly fox movement rates were higher as the number of hours since sunrise increased, both as a linear and quadratic effect (β = 8.67 ± 0.44 SE and β = 1.29 ± 0.44 SE for linear and quadratic effects, respectively). Transient foxes had higher observed mean hourly movement rates across all hours (β = 0.32 ± 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 (β = 0.15 ± 0.09 SE, 95% confidence interval overlaps 0), or substantially improve model fit ($\Delta AIC_c = 0.24$) 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, Fig. 4). 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.

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 3). 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 4). 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, Table 4). 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.

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, Voigt 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). Population density also can strongly influence home range size in red foxes, with home range sizes generally decreasing as population density increases (Trewhella et al. 1988, Šálek et al. 2014). Concurrent population monitoring results suggest that red fox population densities on the island were quite high prior to mange outbreaks (at least 6.26–9.09 foxes/km^2; *Chapter 1*, Robertson et al. 2019). These high population densities likely contributed to the small home range sizes observed during this study. The relatively small geographic area of the island may also have influenced home range sizes, as the entire island (i.e., including the areas on both sides of Old Inlet) encompassed <3000 ha.

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 ha ± 14.63 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 ha ± 34.12 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 versus VHF collars in that 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.

Previous studies in non-barrier island coastal habitats have also 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 pattern also appears to apply 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).

The observed transient behavior of a significant proportion (29%)of GPS-collared 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 in many parts of the study area, 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 patterns, 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. Vegetation removal could 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).

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 also agree with the results of 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 a minimal effect on probability of red fox habitat use. The combined results of these studies suggest that, while coastal red foxes in general prefer dry habitats, selection for anthropogenic features may differ by location.

Mange influenced some but not all aspects of red fox spatial ecology on the island, with mange-affected red foxes using larger core use areas compared to unaffected red foxes. This result suggests that affected animals may be covering more area, potentially as a method of compensating for decreased hunting success, which may arise as a result of the deteriorating body condition associated with advanced cases of mange (Carricondo-Sanchez et al. 2017). Although we did not observe any differences between affected and unaffected red fox habitat selection patterns, previous research suggests that mange also may influence red fox habitat selection. Red foxes suffering from advanced stages of mange in southeastern Norway used areas closer to development 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. 2010). We observed substantial declines in red fox population density on Fire Island following sarcoptic mange outbreaks (*Chapter 1,* 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, resources may be better used to manage vegetation, which will reduce habitat suitability for red foxes while improving suitability for shorebird nesting (Robinson et al. 2019). 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.

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TABLES

Table 1. Model selection table for generalized linear mixed model analysis of home range and core use area sizes for GPS-collared red foxes (n = 33 datasets, 31 individual 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, ΔAIC = difference in AIC value between candidate model and top-ranked model. Only models within 4 ΔAIC_c of the top model are shown.

Area	Model	K	Log Likelihood	AIC_c	ΔAIC_c	Model 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

Table 2. Model selection table for generalized linear mixed model analysis of hourly movement rates for GPS-collared red foxes (n = 33 datasets, 31 individual red foxes) 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, ΔAIC = difference in AIC value between candidate model and top-ranked model. Only models within 4 ΔAIC_c of the top model are shown.

Model	K	Log Likelihood	AIC_c	ΔAIC_c	Model 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

Table 3. Model selection table for within-home range (3^{rd} order) resource selection function analyses for GPS-collared red foxes (n = 33 datasets, 31 individual red foxes) 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, ΔAIC = difference in AIC value between candidate model and top-ranked model.

Model	K	Log Likelihood	AIC_c	ΔAIC_c	Model 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 4. 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 datasets, 31 individual red foxes) 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 of areas closer to a given habitat type than expected, while positive values indicate selection of areas further from a given habitat type than expected. Confidence intervals overlapping zero (marked with a *) indicate no clear directional selection pattern.

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

[a] Using period (day) as the reference level for intercept and main effects

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

FIGURES

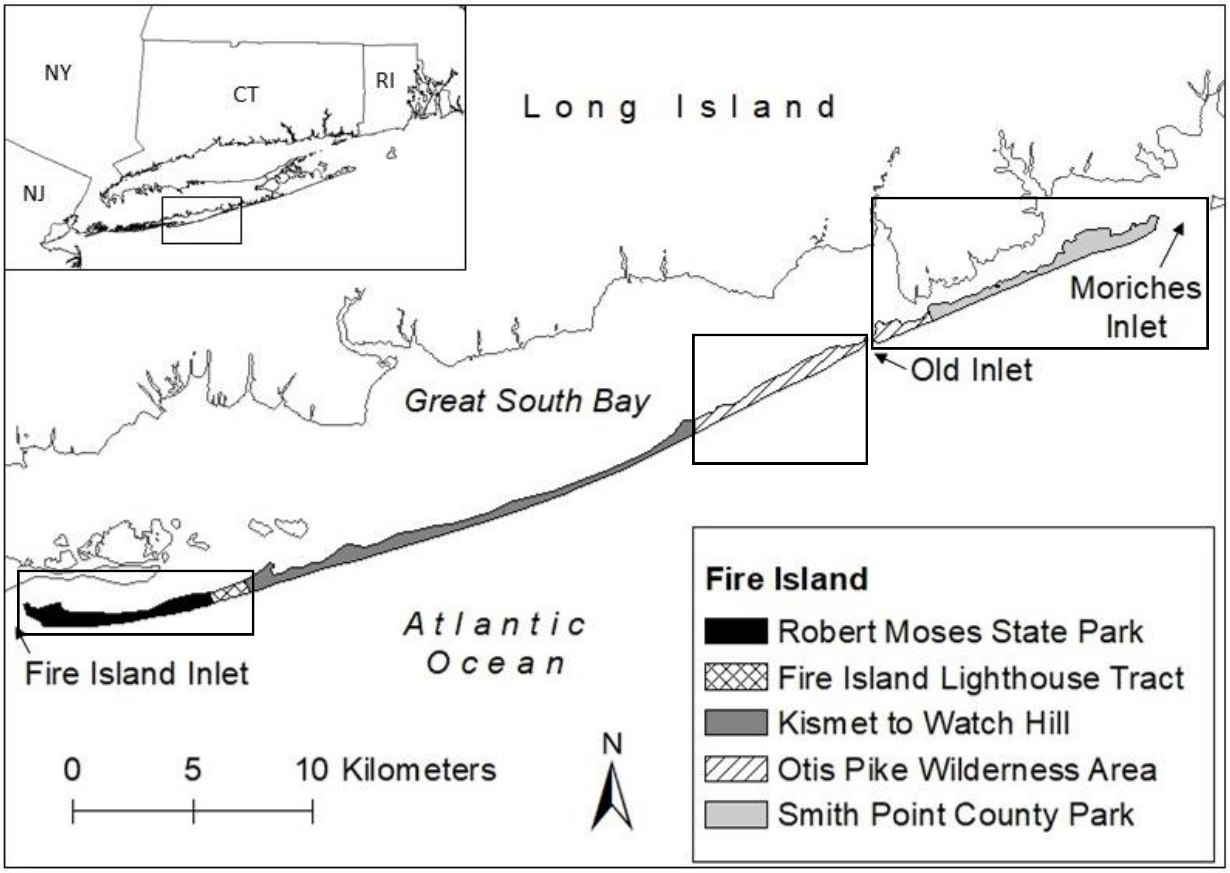

Figure 1. Map of study area on Fire Island, New York. Research efforts were focused in 3 monitoring areas, outlined in boxes, from west to east: 1) Robert Moses State Park and the Fire Island National Seashore Lighthouse Tract, 2) Fire Island National Seashore Otis Pike High Dune Wilderness Area (west of Old Inlet), and 3) Smith Point County Park and Fire Island National Seashore Otis Pike High Dune Wilderness Area (east of Old Inlet). While fox trapping was confined to these three monitoring areas, GPS collars allowed us to follow fox movements as they naturally occurred across all of Fire Island.

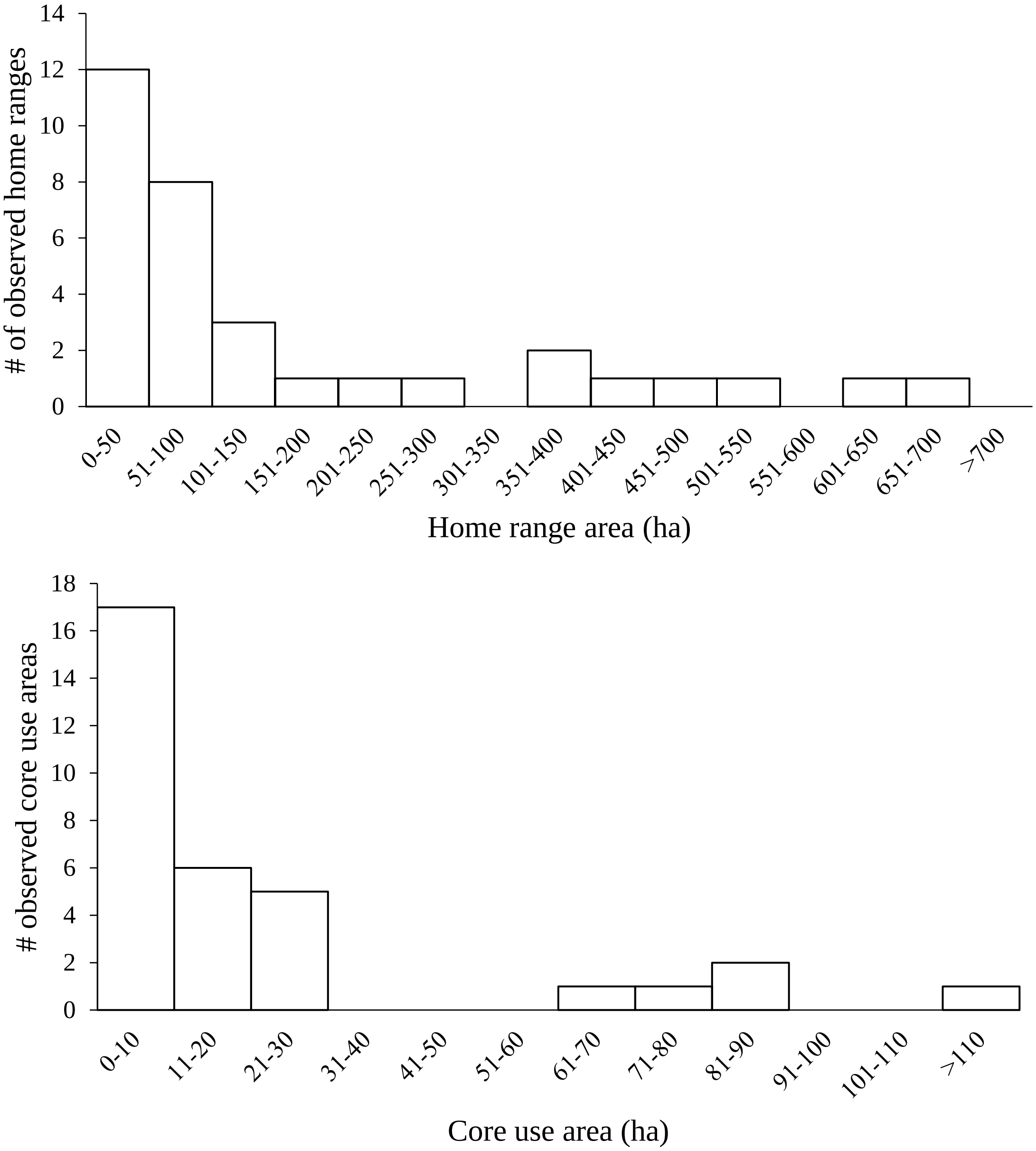

Figure 2. Home range (top) and core use area (bottom) sizes (n = 33) estimated from 31 individual GPS-collared foxes monitored on Fire Island, New York in 2015–2018. 95% and 50% Time Local Convex Hull (T-LoCoH) utilization distribution isopleths were used to represent home ranges and core use areas, respectively.

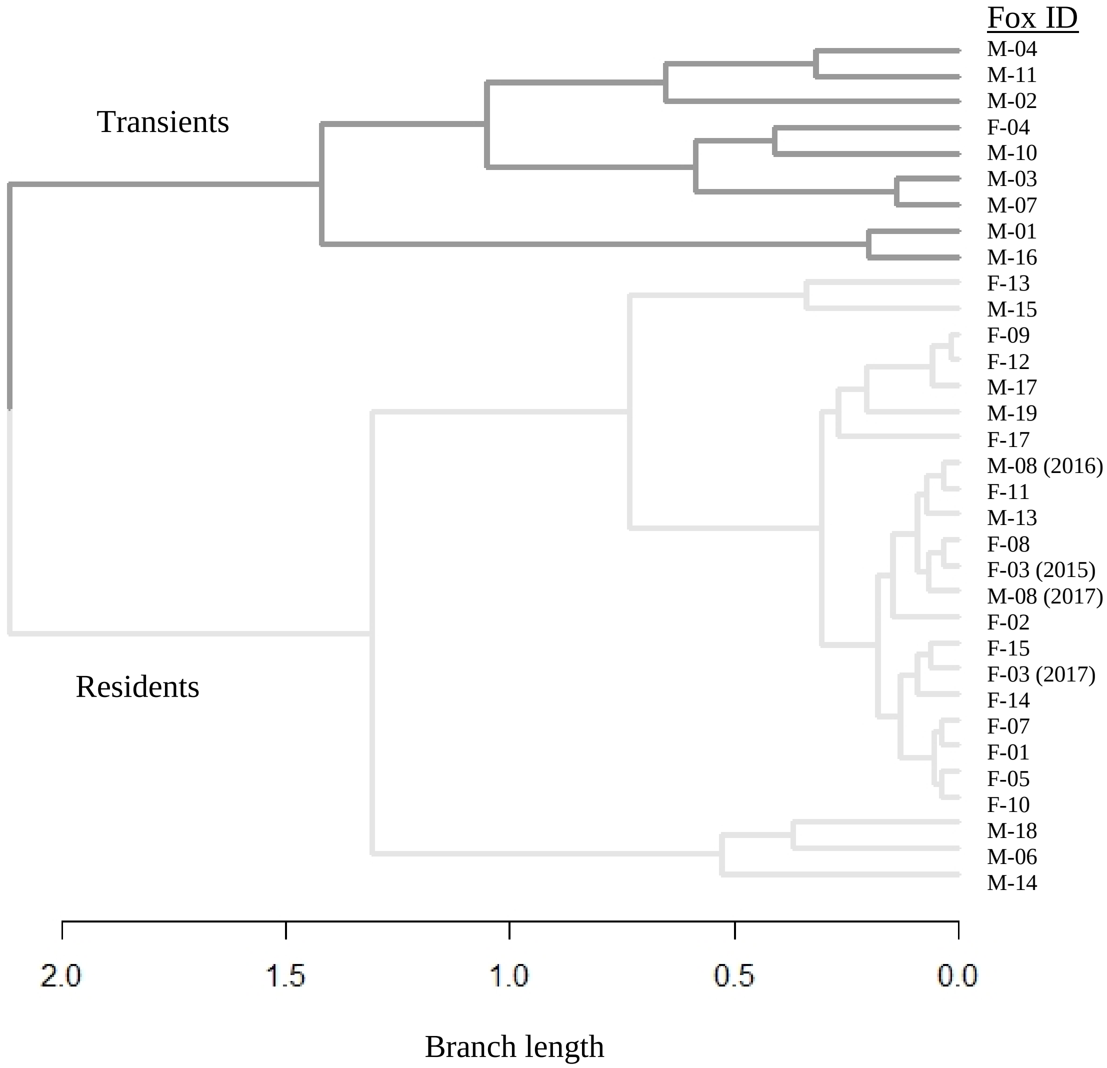

Figure 3. Dendrogram of cluster analysis results used to classify GPS-collared red foxes (n = 31 individual red foxes, 33 datasets) monitored on Fire Island, New York in 2015–2018. We conducted a cluster analyses to sort red foxes into 2 groups based on similarity in home range size and the coefficient of variation of observed distances to home range centroid. We classified red foxes that were grouped together in the cluster analysis based on their small home range sizes (10–165 ha) and lower variation in distance to centroid as residents, and classified red foxes that were grouped together based on their large home range sizes (245–659 ha) and high variation in

distance to centroid 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.

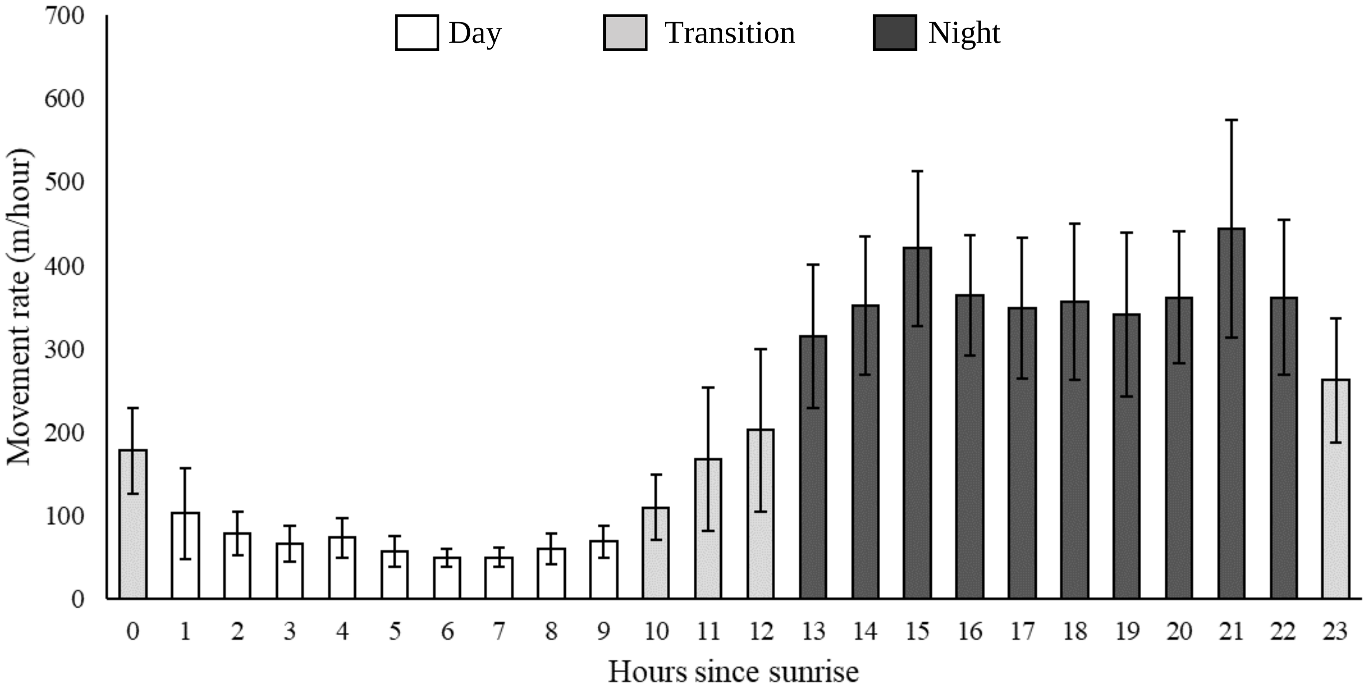

Figure 4. Mean hourly movement rates and 95% confidence intervals (n = 33 datasets, 31 individual red foxes) across all GPS collared red foxes monitored on Fire Island, New York in 2015–2018. We identified 2 diel activity categories based on overlapping confidence intervals among hourly movement rates: 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.

APPENDIX B. SUPPORTING INFORMATION FOR CHAPTER 2

Table B1. Identity, year and season monitored, site captured, resident versus transient categorization, reproductive status, sarcoptic mange infection status, and fate of GPS-collared foxes (n = 36 unique red 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[c]	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[c]	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[c]	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[c]	2017	SP/SU	FINS	-	-	N	Died April 2017 of unknown causes, insufficient data for analyses
M-19[d]	2018	SP/SU	RMFIL	Resident	N	Y	Died May 2018, likely mange
F-17[d]	2018	SP/SU	RMFIL	Resident	N	N	Died May 2018, unknown cause
F-18[c]	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] Excluded from analyses due to insufficient data

[d] <300 locations recorded due to death early in monitoring period

Table B2. Model selection table for preliminary comparisons of univariate generalized linear mixed models of hourly movement rates of GPS-collared red foxes (n = 33 datasets, 31 individual red foxes) 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, ΔAIC = difference in AIC value between candidate model and top-ranked model.

Model	K	Log Likelihood	AIC_c	ΔAIC_c	Model 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

CHAPTER 3.

Using GPS location data to assess potential red fox responses to predator exclosures at piping plover nests

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Using GPS location data to assess potential red fox responses to predator exclosures at piping plover nests

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ABSTRACT Wire cages (‘predator exclosures’) frequently are used to protect shorebird nests from predation. While exclosed nests often have higher survival than unexclosed nests, concerns exist over whether these conspicuous structures might draw increased attention from predators, perhaps increasing risks to adults and newly-hatched chicks. We used location data from GPS-

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collared red foxes (*Vulpes vulpes*) to examine short-term spatial responses of red foxes to predator exclosures and hatching events at piping plover (*Charadrius melodus*) nests. We compared mean distances between red foxes and piping plover nests, and the proportion of red fox locations within a 100-m buffer of these nests, in the 48-hour periods before versus after exclosure set-up, the start of pre-hatch pipping, and hatching. Mean distances from each red fox's locations to nests were similar before versus after exclosure setup ($\bar{x}$ = 641m before, 675m after; permutation test for matched pairs, [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, $T = 0.00$, $P \leq 0.001$, n = 5 foxes) and increased following hatching ($\bar{x}$ = 773m before, 794m after PTMP, $T = 0.00$, $P \leq 0.001$, n = 5 foxes). The proportion of red fox locations within 100-m buffers surrounding nests did not significantly differ before versus after exclosure setup ($\bar{x}$ = 0.01 before, 0.03 after; PTMP, $T = 0.26$, $P = 0.53$, n = 9 foxes), pipping ($\bar{x}$ = 0.03 before, 0.12 after; PTMP, $T = -1.00$, $P = 0.16$, n = 5 foxes), or hatching ($\bar{x}$ = 0.13 before, 0.12 after; PTMP, $T = 0.65$, $P = 0.73$, n = 5 foxes). We conclude that red foxes in our study area did not appear to consistently key in on piping plover nest exclosure setup, pipping, or hatching at the spatial scales considered in our comparisons.

KEY WORDS *Charadrius melodus*, nest exclosure, piping plover, red fox, *Vulpes vulpes*, shorebird

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. 2019). 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, Hunt et al. 2019, Darrah et al. 2020).

One commonly used non-lethal technique to reduce nest predation involves creating a physical barrier between nests and potential predators by surrounding the nest with wire mesh fencing (i.e., setting up a ‘predator exclosure’; Rimmer and Deblinger 1990, Melvin et al. 1992). Fencing is chosen such that the nesting species can easily fit through the gaps between wires, but larger predator species cannot. Empirical comparisons of nest predation rates at exclosed and unexclosed shorebird nests suggest that these exclosures can reduce nest predation and increase hatch success (Maslo and Lockwood 2009, Barber et al. 2010, Dinsmore et al. 2014, Cohen at 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 (*Vulpes vulpes*) 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).

After a red fox has located an exclosed nest, 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 8 of 82 exclosed nests (9.8%) during their study on Westhampton Island, New York, and Barber et al. (2010) reported red fox predation at 2 of 183 exclosed nests (1.1%) 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 also are concerns over whether the hatching process and associated embryonic vocalizations may attract predators to nests. 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, until they have fully penetrated the shell and can emerge. During this time, the chicks may vocalize inside the egg (Gottlieb and Vandenbergh 1968, Freeman and Vince 1974, Kostoglou et al. 2017). These vocalizations, or the parental behaviors 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.

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 versus after exclosure setup, pre-hatch pipping at nests, and nest hatching. 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 period. However, there also was the possibility that red foxes could have been keying in on exclosures or hatching events over shorter periods or smaller spatial scales, which may not have been reflected in their mean distances at the home range scale. Thus, we also tested for changes in the proportion of red fox locations within 100 m of exclosures before versus after these events. If red foxes were attracted to the visual cues of nest exclosures in their home range, we would expect fox locations to be closer to nests on average, and/or a greater proportion of locations would be within the 100-m buffer zone, after exclosure setup, pipping, and hatching than before 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 to nest, or proportion of locations within the 100-m buffer zone, following these events.

STUDY AREA

We conducted this study in Robert Moses State Park and Fire Island National Seashore on Fire Island, New York, which lies off the southern coast of Long Island, New York (Fig. 1). These areas provided important habitat for nesting piping plovers and for other migratory shorebirds (Monk et al. 2020). Natural landcover types on the island included ocean beach, dune and interdune areas of mixed sand and vegetation, shrub/scrub, marsh, and maritime forest. Various developed areas were also present on the island, including paved roads, parking lots, and visitor centers to accommodate the large numbers of visitors present during summer months, as well as numerous small villages interspersed between the park areas.

Managers enacted seasonal beach driving closures and erected string fencing (i.e., ‘symbolic fencing’) to exclude people from nesting areas during the shorebird breeding season on the island in April–August. They also frequently used nest exclosures (Appendix C) to protect piping plover nests from red foxes and other potential predators that were common in the study area, including feral cats (*Felis catus*), domestic dogs (*Canis lupus familiaris*), raccoons (*Procyon lotor*), gulls (*Larus spp*.), and various birds of prey. Opossums (*Didelphis virginiana*), American mink (*Neovison vison*) and long-tailed weasels (*Mustela frenata*) were present in parts of the study area, but were relatively uncommon (K.M. Black, Virginia Tech, unpublished data). Nest exclosures were circular in shape, ~3-m in diameter and ≥122-cm tall, and made of welded wire fencing with horizontal and vertical openings between wires measuring ~5 cm and ~10 cm, respectively. Piping plovers could pass through these openings, while red foxes and other larger animals could not. The fencing was sunk into the ground to prevent predators from digging beneath. Metal t-posts support the exclosure structure and mesh netting covers the top.

METHODS

Red Fox Trapping, GPS Collaring, and Tracking

We captured red foxes with Victor 1½ Soft Catch and Bridger #2 padded foothold traps 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 trapping efforts near 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 red foxes with GPS collars (Quantum 4000E, medium size; Telemetry Solutions, Concord, CA, USA). Collars were programmed to record locations once every 1-2 hours 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, Concord, CA, USA).

We searched for piping plover nests in all areas of suitable dry sand habitat within the study area, surveying each area every 1–3 days using a combination of walking surveys and intensive nest searching in areas where adult piping plovers exhibited parental behavior (Walker et al. 2019, Robinson et al. 2020*a*). We estimated nest initiation dates by counting back 1.5 days per egg present (for partial clutches; Wilcox 1959; Haig and Oring 1988) or by floating eggs (for full clutches, Westerskov 1950), then used these initiation dates to estimate hatch dates. We visited nests every 1–3 days between nest discovery and hatching, and recorded any signs of pipping (i.e., shell fracturing) observed during visits.

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 planned predator exclosure setup and estimated hatch dates 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. Where multiple nests were discovered within a single red fox 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 exclosure set-up, first sign of pipping (based on field observations during nest checks), 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 conservatively excluded locations that fell >10m into the ocean surrounding the island and those with a recorded elevation of >100m (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).

For all analyses, we used the highest frequency location data available for the 48-hour periods before and after the target event. When events did not occur at the predicted times, 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. Exclosure 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- versus post-pipping and 1200 as the cutoff for pre- versus 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 used permutation tests for matched pairs (PTMP; McCune and Grace 2002, Cade and Richards 2005) to compare mean distances from foxes to nests before and after events. In these analyses, we used the mean distance to nest for each red fox as the response variable, period (pre- versus 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 versus 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 period (pre- versus post-event) as the grouping variable. 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 (Cade and Richards 2005), and compared mean distances and data distributions pre- versus post-event to determine the direction of any observed responses.

We also compared the proportion of red fox locations within a 100-m buffer around nests recorded during the 48-hour time periods before versus after exclosure setup, pipping, and hatching. Estimated GPS location error was ≤25m for >95% of red fox locations that were based on >3 satellites 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*b*). Accounting for this ≤25-m error, a 100-m buffer should include any locations within 0–125 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 <100m from the nest. We compared the proportions of locations in this buffer from each 48-hour period before versus after each type of event using permutation tests for matched pairs (PTMP; McCune and Grace 2002), conducted using Blossom Statistical Package (Cade and Richards 2005), and compared proportions and data distributions pre- versus post-event to determine the direction of any observed responses.

RESULTS

Red Fox Trapping, GPS Collaring, and Tracking

We captured and GPS-collared 5 red foxes in 2016 and 5 red foxes in 2017 whose home ranges overlapped with plover nesting areas and for whom we successfully reprogrammed GPS collars to the high frequency schedule. 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 year, geographic shift in that fox's territory between breeding seasons (~500m westward shift in home range boundaries between 2016 and 2017 breeding seasons), and shift in plover nest locations between nesting seasons.

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 1). Much of this variation was due differences between predicted and actual dates for exclosure setup, pipping, and hatching at some nests, which resulted in temporal mismatch between our high frequency data collection and the 48-hour window surrounding those events at some nests.

Assessing Spatial Response

Mean distances from red fox locations to nests were similar before versus 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, $T = 0.00$, $P \leq 0.001$, n = 5 foxes) and increased following hatching ($\bar{x}$ = 773m before, 794m after; PTMP, $T = 0.00$, $P \leq 0.001$, n = 5 foxes; Table 2, Fig. 2).

Despite the lack of a change in mean distances to nest following exclosure setup when all foxes were considered as a group, our individual-level MRPP comparisons identified shifts in distances to nest for 4 of the 9 red foxes included in our analyses: 2 red foxes used 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 used 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 2). We observed similar variation among individuals in our MRPP comparisons surrounding pipping: 2 of 5 red foxes used 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 used 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 2). None of the 5 red foxes included in our hatching comparisons showed significant differences in distances from their locations to nests before versus after hatching.

The proportions of red fox locations within 100-m buffers surrounding nests were low (mean proportion across all foxes < 0.13 for all pre- and post-event periods) and did not differ before versus 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 3, Fig. 3).

DISCUSSION

In this study, red foxes did not exhibit consistent spatial responses to exclosure setup. We observed some differences in red fox space use surroundingpipping and hatching at piping plover nests, but it is unclear whether these differences were driven by events at nests or by other factors. We observed a decrease in mean distance from red fox locations to nests within their home ranges in the 48-hr period following pipping, which 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 from red fox locations to nests post-pipping was still > 500m. Similarly, the observed increase in mean distance from red fox locations to nests in the 48-hr period following hatching is consistent with the idea that any potential attraction during pipping may dissipate as chicks emerge from eggs and leave the nest area, but the mean distances to nest were still >750m during pre-hatch and post-hatch periods.

We did not find evidence of a relationship between red fox space use in the 100-m buffer surrounding 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, which lies directly east of the Fire Island National Seashore portion of the study area, during the 2015 and 2018 piping plover breeding seasons, suggesting that red fox responses to nest exclosures may vary from year to year and between management areas or among individual foxes. In 2015, at least one red fox in Smith Point County Park learned to penetrate nest exclosures, prompting the removal of nest exclosures partway through the breeding season; none of the nests survived to hatch following exclosure removal (C.C. Robertson et al., Virginia

Tech, unpublished report). In response to digging at nests in 2018 at Smith Point County Park, managers temporarily stopped exclosing nests in the park, but resumed exclosure use following the depredation of 6 unexclosed nests; red foxes were suspected in the depredation of 4 of these nests, based on tracks found in the immediate vicinity (L.F. Hermanns et al., Virginia Tech, unpublished report). Considered alongside our findings, these findings suggest that, while most foxes do not appear to key in on exclosures, there are clearly some red foxes that do find and dig at or climb into exclosures.

It is 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 2*/K.M. Black, Virginia Tech, unpublished data) estimated a mean hourly movement rate of 216.3 m/hr ± 8.7 m/hr (SE) across all hours, and a mean hourly movement rate of 366.5 m/hr ± 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 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 piping plover nests take advantage of both GPS collar and remote camera data collection approaches. Concurrent remote camera monitoring of a subset of piping plover nests within the study area and in Smith Point County Park and nearby Cupsogue Beach County Park documented regular red fox visitation at exclosed nests, with 19 red fox detection events across all camera-monitored nests ($n = 14$) in 2016 and 9 red fox detection events across all camera-monitored nests ($n = 27$) in 2017, but none of the foxes in these nest camera photographs had GPS collars (C.C. Robertson et al., Virginia Tech, unpublished report; C.C. Robertson, Virginia Tech, unpublished data).

In the absence of clear evidence that red foxes are drawn to nest exclosures, we recommend continued exclosure use within our study area, since whether or not a nest was exclosed was the strongest predictor of piping plover nest survival during the study (C.C. Robertson, 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. We acknowledge that the low number of GPS-collared foxes included in these comparisons may have influenced our results, and recommend that future studies include more GPS-collared animals if possible.

To our knowledge, this is the first study to use GPS location data to examine spatial responses of predators to nest exclosures, pipping, 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. These studies highlight the variety of potential applications of GPS location data to the study of predator-prey interactions. We recommend further research on these potential applications, and anticipate that advances in GPS tracking technology will enable more detailed investigations in years to come.

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TABLES

Table 1. 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.

			Exclosure		Pipping		Hatching	
Year	Fox[a]	Nest ID[c]	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[b]	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[d]	190	54				
2017	M-08[b]	214	6	128	20	0[e]	0[e]	0[e]
2017	M-17	211[d]	183	52				

[a] M denotes males, F denotes females

[b] This fox was captured and monitored during both 2016 and 2017; the 2 location datasets were treated as independent in analyses

[c] Unique nest identifier used in field monitoring and data management (C.C. Robertson et al., Virginia Tech, unpublished report)

[d] Nest failed in between exclosure setup and estimated hatch date

[e] Collar malfunction resulted in no usable data during these periods

Table 2. 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 ((post-pre)/pre)*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.

			Exclosure				Pipping				Hatching			
			Mean or Δ Distance (m)				Mean or Δ Distance (m)				Mean or Δ Distance (m)			
Year	Fox[a]	Nest[b]	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 (C.C. Robertson et al., Virginia Tech, unpublished report)

[c] Nest failed in between exclosure setup and estimated hatch date

^ denotes *P* ≤ 0.05 in individual multiple response permutation procedure for matched pairs (PMTP) comparison

* denotes *P* ≤ 0.05 in overall permutation test for matched pairs (PMTP) comparison

Table 3. 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.

			Exclosure			Pipping			Hatching		
			Proportion or Δ Proportion of points ≤ 100 m of nest			Proportion or Δ Proportion of points ≤ 100 m of nest			Proportion or Δ Proportion of points ≤ 100 m of nest		
Year	Fox[a]	Nest[b]	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

FIGURES

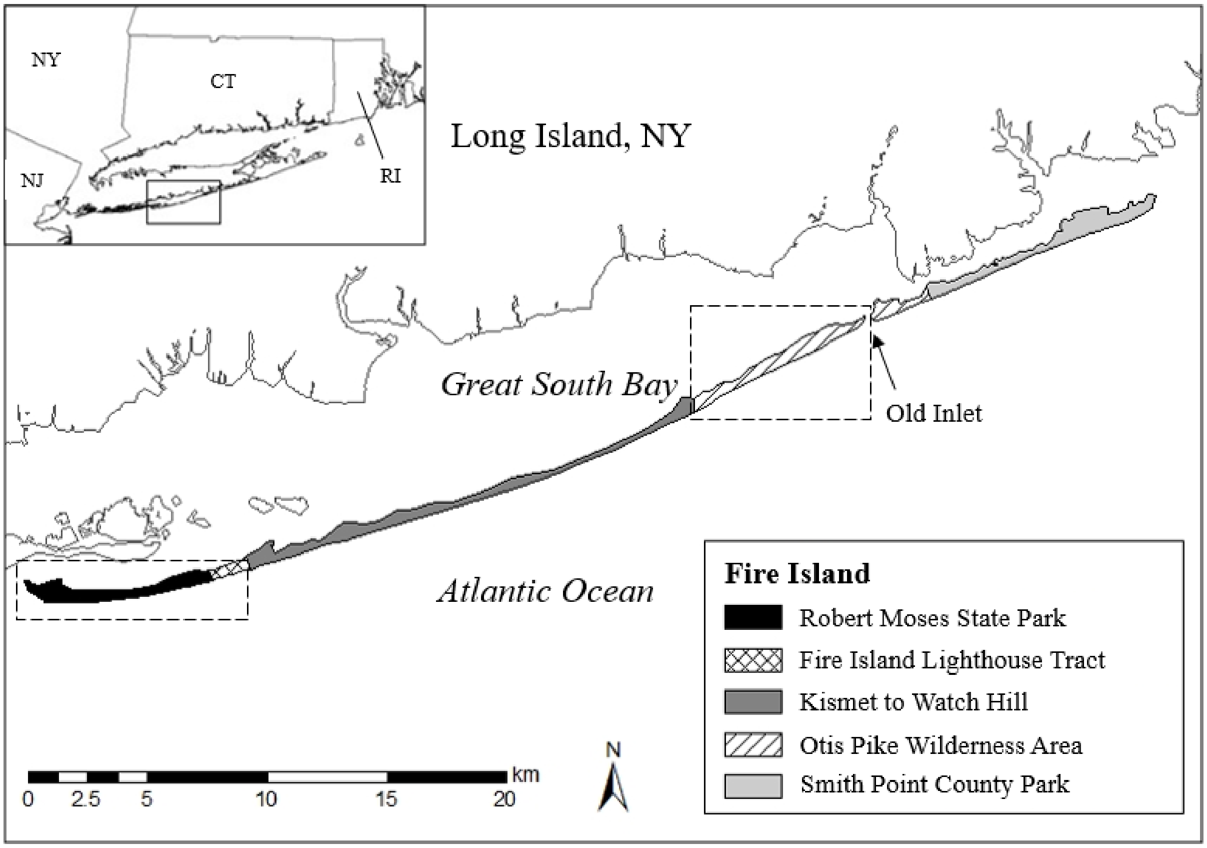

Figure 1. Map of study area on Fire Island, New York. Research activities, conducted in 2016–2017, were focused in 2 geographic areas on the island (outlined in boxes): 1) Robert Moses State Park and the Fire Island National Seashore Lighthouse Tract, and 2) Fire Island National Seashore Otis Pike High Dune Wilderness Area (west of Old Inlet).

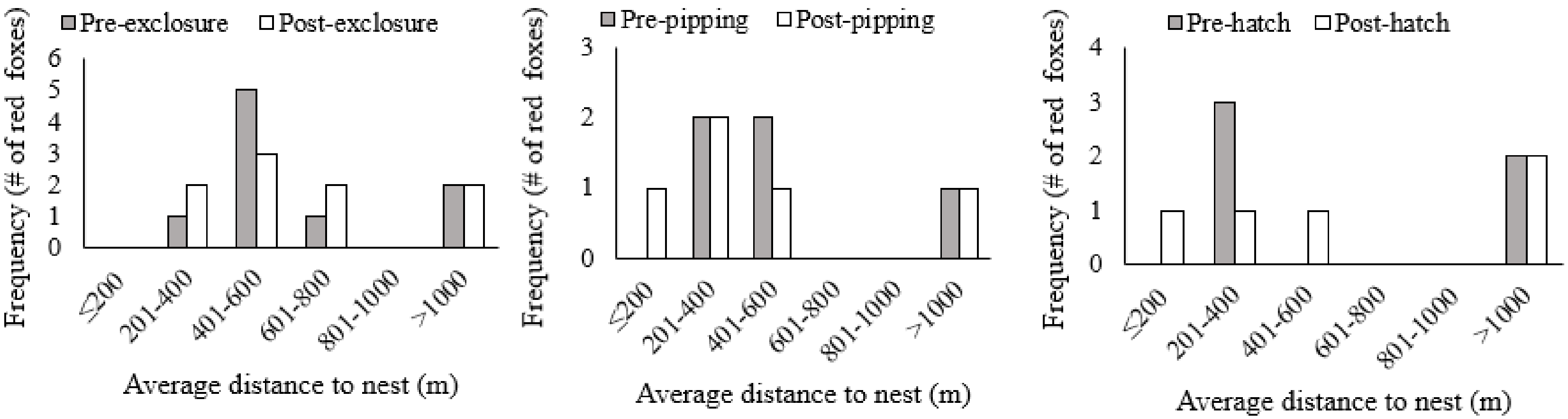

Figure 2. Distribution of mean distances from GPS-collared red fox locations to piping plover nests during 48-hr periods before vs. after exclosure setup (left, n = 9), pipping (middle, n = 5), and hatching (right, n = 5) on Fire Island, New York in 2016–2017.

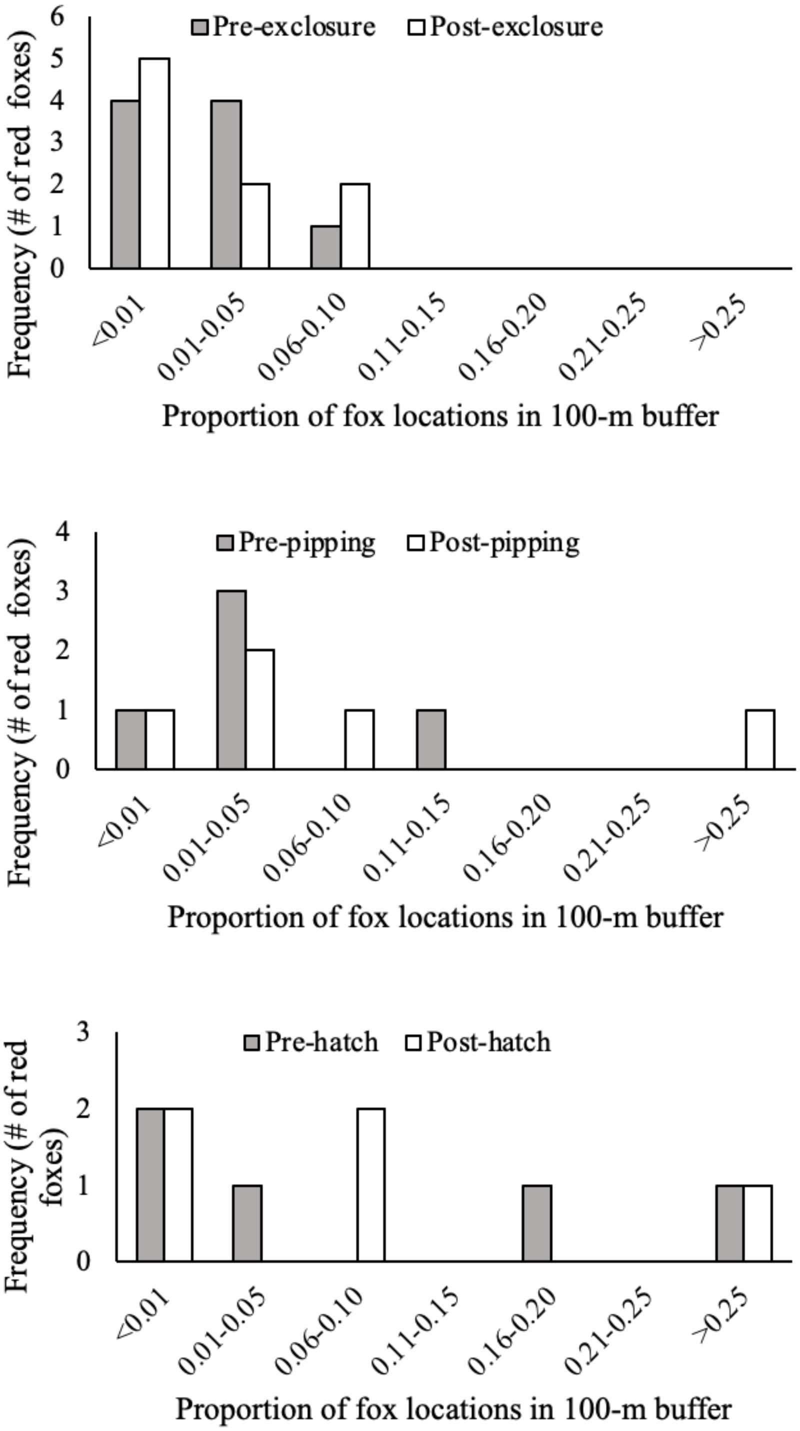

Figure 3. Distribution of the proportions of GPS-collared red fox locations within 100-m buffers surrounding piping plover nests during 48-hr periods before vs. after exclosure setup (top, n = 9), pipping (middle, n = 5), and hatching (bottom, n = 5) on Fire Island, New York in 2016–2017.

APPENDIX C. ADDITIONAL INFORMATION ON NEST EXCLOSURES USED IN THE STUDY AREA

Figure C1. Photo of a typical exclosure set up around a piping plover nest (circled) on Fire Island, New York in 2016–2017. Exclosures were circular in shape, measuring ~3 m in diameter and ≥122 cm tall, and made of welded wire fencing with horizontal and vertical openings between wires measuring ~5 cm and ~10 cm, respectively. Piping plovers could easily pass through these openings, while red foxes, raccoons, feral cats, and most other piping plover predators could not. The surrounding fencing was sunk into the ground to prevent predators from digging beneath. The top was made of flexible plastic bird netting rather than rigid wire mesh to discourage aerial predators from perching. Metal t-posts supported the exclosure structure. Photo: K. Black.

CHAPTER 4.

Red fox dietary ecology in a semi-urban coastal ecosystem

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Red fox dietary ecology in a semi-urban coastal ecosystem

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Red fox (*Vulpes vulpes*) diets have been described in a variety of locations, but little is known about red fox dietary ecology in Atlantic coastal ecosystems of the U.S., where red foxes are frequently managed to protect piping plovers (*Charadrius melodus*) and other bird species of conservation concern. We used fecal diet analyses and den prey surveys to study the diet of red foxes on Fire Island, NY. We also compared encounter frequency of anthropogenic foods at breeding dens based on relative proximity to development and estimated litter sizes to determine whether anthropogenic food resources might be subsidizing the red fox population. We identified 27 orders of prey in red fox scats, of which Rodentia (rodents, 43% of scats), Coleoptera (beetles, 38%), and Decapoda (crabs and other crustaceans, 29%) were the most frequently represented taxonomic orders. Bird remains (from multiple orders) were found in 35% of scats. Anseriformes (ducks, geese, swans; 6% of scats), Passeriformes (perching birds, including songbirds; 6%), and Charadriiformes (shorebirds, including gulls, terns, plovers, 3%) were the most common bird orders identifiable in red fox scat. We did not find any clearly identifiable piping plover remains in red fox scats, but we did find a pair of piping plover leg bands in a domestic cat scat. Fish (89% of dens with food items), shellfish (67%), and mammal remains (67%) were found outside of the highest proportion of red fox dens with food items. At the lowest identifiable taxonomic level, skates (Family Rajidae, 89% of dens with food items) and Atlantic surf clams (*Spisula solidissima*, 67%) were found outside the highest proportion of dens, and made up 61% of all food items recorded at dens. Of the mammal remains at dens, white-tailed deer (*Odocoileus virginianus*) was the most frequently found species (50% of dens with food items), but only made up 3% of all food items recorded at dens. We found bird remains, primarily gulls (*Larus spp*.), outside of 44% of dens with food items. We found anthropogenic items, primarily consisting of food wrappers and other packaging, in 16% of red fox scat samples and outside of 50% of dens with food items, making up 12% of all items recorded at dens. Estimated litter sizes were positively correlated with the rate of fish accumulation at secondary dens, indicating that fish may represent an important food source for kits as they grow. Our findings suggest that although red fox predation is a concern for piping plover conservation based on other studies, plovers and other shorebirds were not a major prey item for red foxes on the island during our study.

Key words: Anthropogenic food subsidies, diet, red fox, urban ecology, *Vulpes vulpes*

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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 also will 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 red fox scat, occurring in 43.3% and 37.8% of samples, respectively. Marine resources, such as fish, aquatic macroinvertebrates, and washed-up carrion from marine mammals and seabirds may also play an important role in the diets of coastal red foxes, as they have been shown to be consumed by a wide range of terrestrial mammals living in coastal settings (Carlton and Hodder 2003). In some cases, these marine resources may directly and indirectly subsidize coastal mesopredator populations, potentially impacting terrestrial prey species (Rose and Polis 1998, Killengreen et al. 2011).

Red fox diets in developed coastal areas also 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. 2009). 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. 2019). 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 et al. 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 by supporting a larger population of predators than could persist on natural food sources alone, and should be considered in management planning.

The goals of this study 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 hypothesized that consumption of anthropogenic and avian resources would be higher in spring and summer months, reflecting seasonal trends in human and migratory shorebird presence on the island. We also conducted den prey item surveys to provide a secondary index of red fox dietary composition on the island, as we hypothesized that some food items may be under-represented in traditional fecal dietary analyses. Finally, we examined the relationships among anthropogenic food waste at dens, proximity to development, and litter size to determine whether anthropogenic resources and angler discards 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.

MATERIALS AND METHODS

Study area.— Fire Island is a 50-km long barrier island on the southern coast of Long Island, New York. It is currently separated into two sections by Old Inlet, a historic inlet that reopened during Hurricane Sandy in 2012 (Fig. 1). The island is a mosaic of county, state, and national park areas intermixed with small villages. Park areas include a federally designated wilderness area and developed visitor areas and managed beachfronts. The entire island is home to ~300 year-round residents, but receives additional seasonal residents and 2-3 million visitors per year, primarily during the May-August vacation season (NPS 2017). Major undeveloped habitat types on the island include sparsely vegetated sandy beach, dune, and interdune habitats as well as thick shrub/scrub patches, maritime forest, and bayside marsh (Fig. 2). Red foxes were the only wild canid present on the island during the study; domestic cats (*Felis catus*), domestic dogs (*Canis lupus familiaris*), and raccoons (*Procyon lotor*) were also present and widespread within the study area (Robertson et al. 2019). Opossums (*Didelphis virginiana*) were present but relatively uncommon in some parts of the island during parts of the study, as were American mink (*Neovison vison*) and long-tailed weasels (*Mustela frenata*; K.M. Black, Virginia Tech, unpublished data). Our research was focused in 3 areas on the island: 1) Robert Moses State Park and the Fire Island National Seashore Lighthouse Tract, 2) Fire Island National Seashore Otis Pike High Dune Wilderness Area (west of Old Inlet), and 3) Smith Point County Park and Fire Island National Seashore Otis Pike High Dune Wilderness Area (east of Old Inlet; Fig. 1).

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 (*Chapter 2*/

Black et al. *in prep b*) 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 (Fig. 2). 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; see Appendix D, Table D1). Additional fresh scat samples were collected opportunistically throughout the year during concurrent research 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 research activities in the study area, including GPS-collaring and ear-tagging and tracking of adult red foxes in the study area (*Chapter 2*/Black et al. *in prep b*). 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.

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 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 (see Appendix D, SD1), 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).

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 mean number of categories, orders, and species consumed per individual and the frequency of occurrence of different taxonomic orders in individual diets.

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 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. Assuming the same rate of correct identification of source species observed in samples that yielded a source species identification, <3 of these probable red fox samples may have originated from another species.

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 1). 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 1). 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%).

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) and 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 (Fig. 3). 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.

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 calculated mean of 6.67 ± 0.62 SE different categories of prey consumed, 11.33 ± 1.03 SE different orders, and

12.33 ± 1.03 SE different species/lowest identifiable taxonomic levels consumed per individual. Frequency of occurrence of different taxonomic orders did not appear to vary widely across individuals, suggesting fairly similar diets, although small sample sizes resulted in large confidence intervals surrounding estimates (see Appendix D, Fig. D1).

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 (*Chapter 1/*Black et al. *in prep a*).

Fish (89% of dens with food items), shellfish (67%), and mammal (67%) remains were found outside the highest proportion of dens (Table 2). 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 2). 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 2). 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.

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 positively correlated to litter sizes at secondary dens (Spearman's rank correlation coefficient: $\rho_{3} = 0.95$, $P = 0.01$, n = 5), and marginally positively correlated with litter sizes at natal dens (Spearman's rank correlation coefficient: $\rho_{11} = 0.52$, $P = 0.07$, n = 13; Fig. 4).

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 ≤ 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 2011and 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/km^2, 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 large, the contrast becomes more apparent when broken down by order and family. Similar to Peterson et al. (2020), we found passerine bird remains most often in scats, but at a much lower frequency, with their study reporting 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 next most 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

11.1% 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) and inclusion of samples collected in a wider range of habitat types and geographic areas likely contributed to the differences in results between our study and that of Peterson et al. (2020). Overall, these results suggest that consumption of birds by coastal red foxes is frequent, with the exact taxonomic breakdown of species consumed varying across sites and habitat types.

Despite red fox harassment at and predation of nests at Smith Point County Park in 2015 (Monk et al. 2015) and 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. It is possible that depredation of nests may have occurred but not been detected, either due to a lack of identifiable remains in scats, or due to imperfect detection of scats during transect surveys. Further investigation of scat detection rates and detection of avian remains in scats in controlled feeding trials could help quantify this probability of non-detection if piping plovers were consumed.

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, considered alongside the observed depredation of nests at Smith Point County Park in 2015 and 2018, suggests that red fox predation of piping plover adults and chicks is opportunistic and variable across years and sites, 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 higher following red fox population declines in the study area due to mange outbreaks(*Chapter 1/*Black et al. *in prep a,* 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 by red foxes 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. This finding is in line with previous studies showing that access to marine resources can positively influence predator population sizes and densities. For example, Rose and Polis (1998) found that coyote population densities in Baja California were up to 13.7 times denser at coastal sites compared to inland sites, based on track and scat counts and other indices of abundance.

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 research 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.

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TABLES

Table 1. 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
Larus spp.			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	
Colinus virginianus			<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	
Dysdera crocata			<0.01
Order Coleoptera		0.38	
Family Histeridae			<0.01
Acritus spp.			<0.01
Family Carabidae			0.03
Calasoma scrutator			<0.01
Pterostichus spp.			<0.01
Family Coccinellidae			
Epilachna borealis			<0.01
Family Curculionidae			<0.01

Dendroctonus spp.			<0.01
Family Elateridae			<0.01
Melanotus spp.			0.01
Family Lucanidae			0.01
Family Scarabaeidae			0.04
Phyllophaga spp.			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
Amblyomma americanum			0.01
Dermacentor spp.			<0.01
Dermacentor variabilis			0.11
Ixodes scapularis			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	
Odocoileus virginianus			0.12

Order Carnivora	0.12	
Felis catus		<0.01
Procyon lotor		0.07
Family Mustelidae		0.02
Mustela frenata		<0.01
Neovison vison		0.01
Unidentified Carnivora		0.01
Order Chiroptera	0.02	0.02
Order Didelphimorphia	0.02	
Didelphis virginiana		0.02
Order Eulipotyphla	0.04	
Scalopus aquaticus		0.01
Family Soricidae		0.01
Blarina brevicauda		0.01
Blarina spp.		<0.01
Sorex cinereus		0.01
Order Lagomorpha	0.08	
Sylvilagus floridanus		0.08
Order Rodentia	0.43	
Family Cricetidae		0.01
Microtus pennsylvanicus		0.04
Microtus spp.		0.09
Ondatra zibethicus		0.04

Peromyscus leucopus			0.02
Peromyscus maniculatus			0.01
Peromyscus spp.			0.03
Family Muridae			0.01
Mus musculus			0.01
Rattus norvegicus			0.02
Rattus rattus			0.01
Rattus spp.			0.04
Family Dipodidae			<0.01
Napaeozapus insignis			0.03
Zapus hudsonius			0.01
Family Sciuridae			
Sciurus carolinensis			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	
Emerita talpoida			0.01

Libinia emarginata			0.02
Ocypode spp.			<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	
Prunus maritima			0.02
Prunus spp.			<0.01
Unidentified vegetation		0.65	0.65
Unknown	0.23	0.23	0.23

Table 2. 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		
Larus spp.					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		
Prionotus spp.					0.11	0.01

Order Squaliformes			0.11	0.02		
Squalus acanthias					0.11	0.02
Unidentified fish, Superclass Osteichthyes			0.39	0.09	0.39	0.09
Mammal	0.67	0.06				
Order Artiodactyla			0.50	0.03		
Odocoileus virginianus					0.50	0.03
Order Carnivora			0.11	0.01		
Procyon lotor					0.11	0.01
Order Rodentia			0.17	0.01		
Peromyscus spp.					0.06	<0.01
Sciurus carolinensis					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		
Malaclemys terrapin					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		
Geukensia demissa					0.11	0.01

Order Venerida			0.67	0.23		
Spisula solidissima					0.67	0.23
Unknown	0.06	<0.01	0.06	<0.01	0.06	<0.01

FIGURES

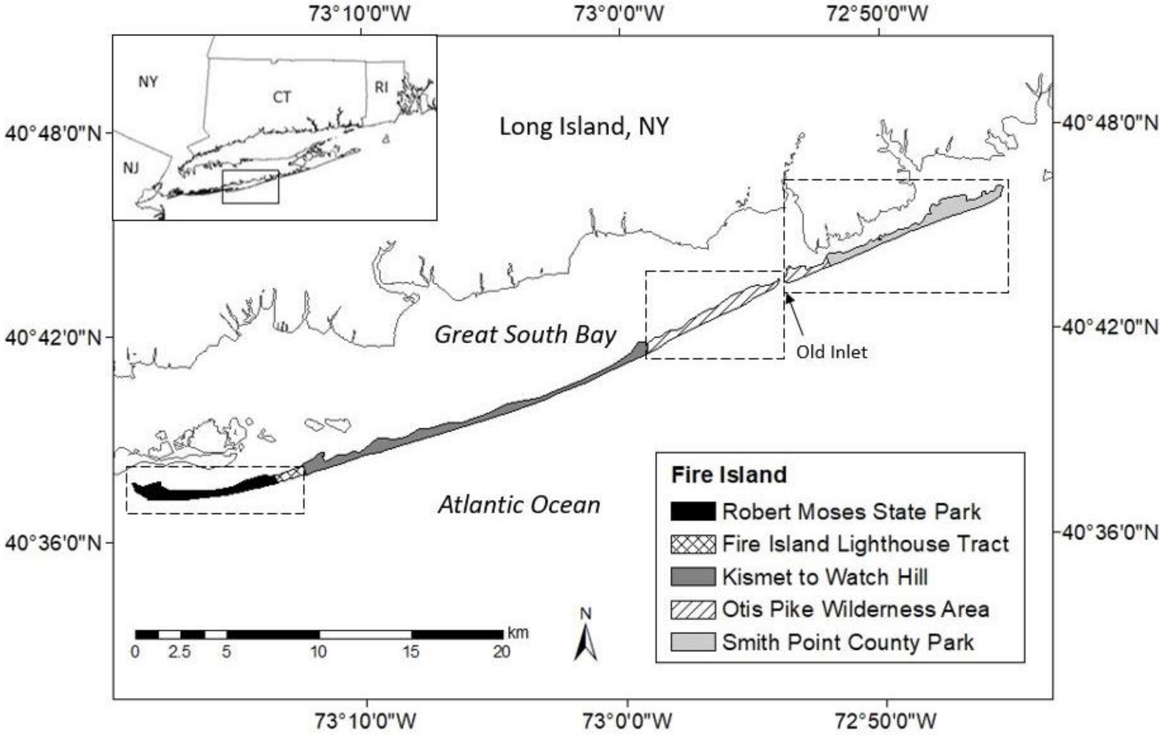

Figure 1. Map of study area on Fire Island, New York. Research efforts in 2016–2019 were focused in 3 geographic areas, outlined in dashed boxes: 1) Robert Moses State Park and the Fire Island National Seashore Lighthouse Tract, 2) Fire Island National Seashore Otis Pike High Wilderness Area (west of Old Inlet), and 3) Smith Point County Park and Fire Island National Seashore Otis Pike High Dune Wilderness Area (east of Old Inlet).

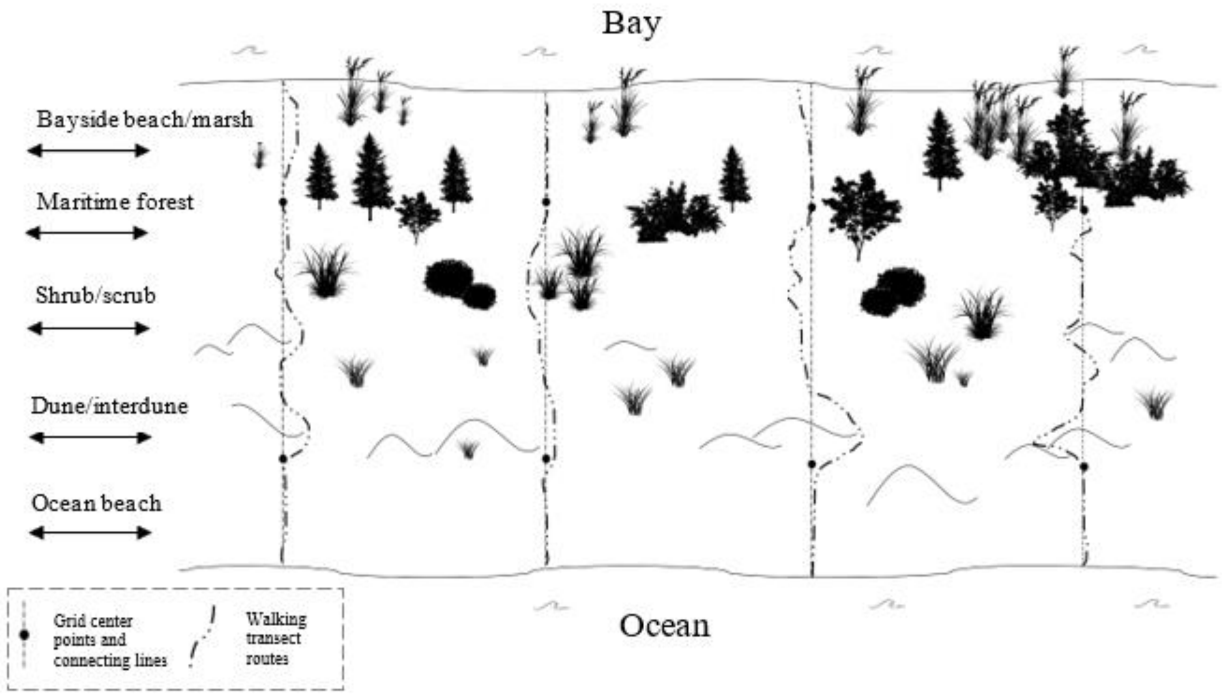

Figure 2. Diagram illustrating habitat types and transect surveys conducted on Fire Island, New York in 2016–2019. We followed game trails, edges, and other likely wildlife travelways along general north-south transect lines based on a 300-m grid overlay of the study area. These transects spanned all passable habitat types within each 300-m section of the study area.

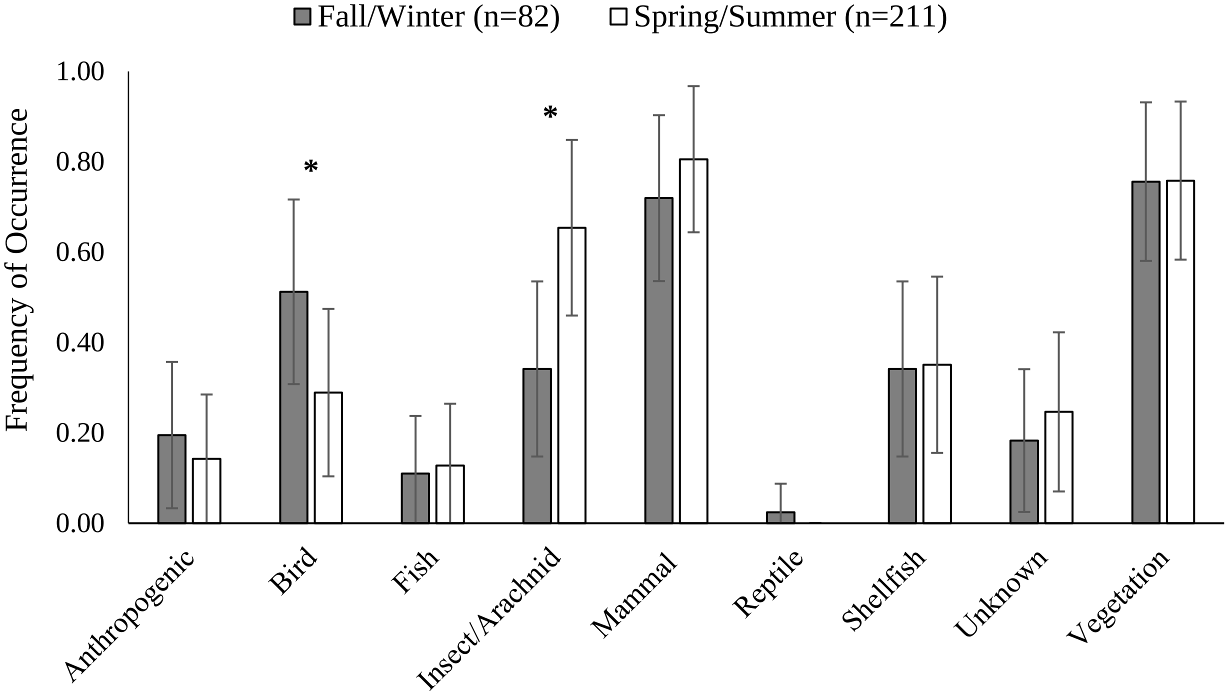

Figure 3. Seasonal comparison of frequency of occurrence by scat sample, defined as the proportion of scat samples that contained at least one item in a given category, for broad categories of food items found in fecal dietary analysis of red fox scat samples (n = 223) collected opportunistically, during systematic surveys, and at den sites on Fire Island, New York in 2016–2019. Error bars indicate binomial 95% confidence intervals. * indicates Pearson's chi-square $P < 0.05$ between seasons.

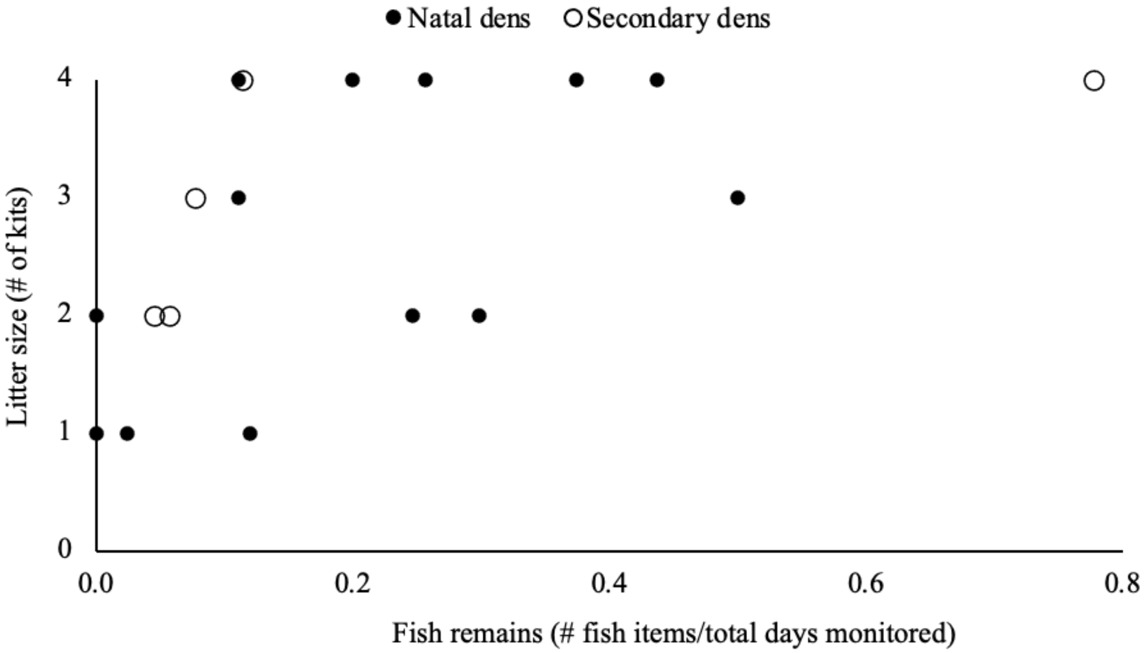

Figure 4. Relationship between litter size and the amount of fish remains recorded during prey item surveys at red fox dens (n = 18) monitored on Fire Island, New York during the 2016 and 2017 breeding seasons. We used remote camera photos and in-person observations at dens, along with information from concurrent GPS tracking of adult red foxes, to classify dens as either natal dens (used early in denning season and in weeks following parturition, typically active through late May; n = 13) 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; n = 5). Dens where no prey items of any kind were recorded (n = 8) are not included in this figure.

APPENDIX D: SUPPLEMENTARY DATA FOR CHAPTER 4

Table D1. 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

SD1. 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

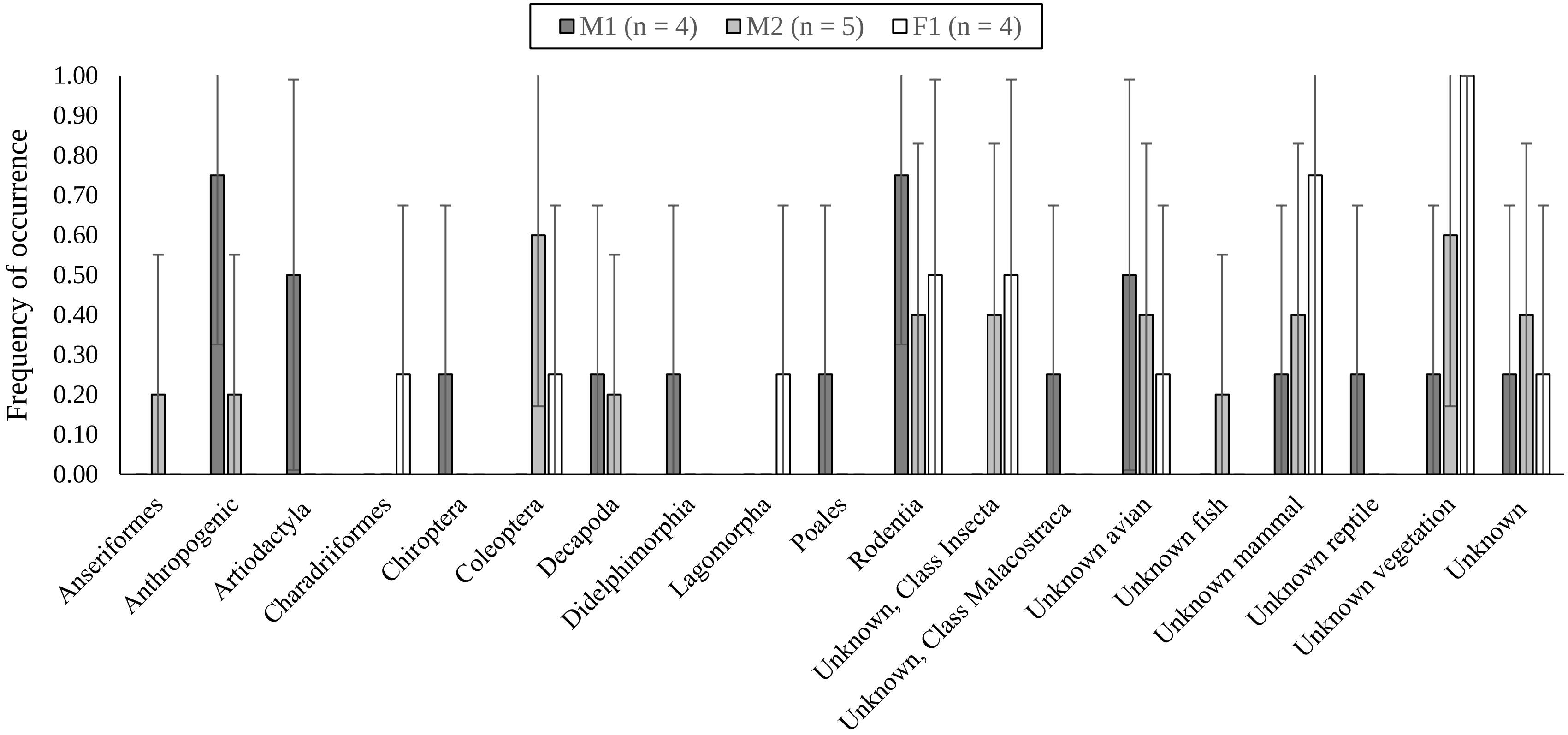

Figure D1. Comparison of frequency of occurrence by scat sample, defined as the proportion of scat samples that contained at least one item in a given category, for different taxonomic orders of food items found in fecal dietary analysis of scat samples collected from 3 different genetically-identified red foxes (n = 13 scats total) on Fire Island, New York in 2016–2019. 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 figure. Error bars indicate binomial 95% confidence intervals.

CONCLUSION

The goal of this dissertation was to quantify key aspects of red fox population, spatial, and dietary ecology and interactions with threatened piping plovers on Fire Island, New York in order to guide red fox predation management efforts to benefit piping plover population recovery. We monitored red foxes on Fire Island, New York from June 2015–February 2019, as part of a larger project monitoring piping plovers and their response to shoreline stabilization activities on the island and on nearby Westhampton Island. Considered alongside the findings of concurrent piping plover (Robinson 2020, Walker 2020) and vegetation monitoring within the study area (Bellman 2019), this work has allowed for a rare side-by-side study of a threatened shorebird, one of its primary predators, and the surrounding environment.

This is one of few studies of red fox ecology in a barrier island ecosystem, and the first, to our knowledge, that examines red fox population dynamics, spatial ecology, and diet on a barrier island over multiple years and using a variety of methods, including GPS-collaring of red foxes, remote camera surveys, den monitoring, and noninvasive genetic analyses using fecal samples. Moving forward, this information can be incorporated into red fox and piping plover management strategies to increase piping plover reproduction and survival on Fire Island and sustain red fox populations, depending on the goals of managers. Below, I discuss the key findings from this study, highlight management implications, and make recommendations for future work.

KEY FINDINGS

Chapter 1: Sarcoptic mange as a driver of red fox population dynamics in a coastal ecosystem

- Red fox trap success (remote camera detections/100 trap nights) decreased by 80-100% following mange outbreaks at each site.
    - Piping plover chick survival was higher following mange outbreaks, when red fox trap success was lower (Robinson 2020).
- Red fox occupancy remained high (≥0.82) as long as foxes were present, regardless of changes in minimum population density.
- Minimum red fox abundance and density decreased sharply following mange outbreaks.
    - Minimum red fox densities at each site ranged from 3.38–9.09 foxes/km^2 before outbreaks, 0.26–6.26 foxes/km^2 during outbreaks, and 0–0.17 foxes/km^2 following outbreaks.
- Complete reproductive failure occurred following mange outbreaks at each site.
    - A rebound had not yet been observed at the time of completion of this research in February 2019.
- Survival rates of GPS-collared foxes during tracking periods (4–6 months) ranged from 0.75–1 before the mange outbreaks, but fell to 0–0.38 during mange outbreaks.
- Of the 14 GPS-collared/ear-tagged adult red foxes that died 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).

Chapter 2: Red fox home range, activity patterns, and habitat selection on an Atlantic barrier island

- GPS-collared red fox home range sizes (95% time local convex hull [t-LoCoH] isopleths) averaged 164.44 ha (33.31 ha SE), ranging from 10.09 ha to 658.55 ha.
  - Males used larger home ranges, as did red foxes monitored in fall/winter compared to those monitored in spring/summer.
- Core use area sizes (50% t-LoCoH isopleths) averaged 25.68 ha (8.51 ha SE), ranging from 0.38 ha to 267.79 ha.
  - Males and red foxes affected by mange used larger core use areas than females and mange-free foxes.
- Twenty-two of 31 GPS-collared red foxes maintained distinct territories throughout the monitoring period, while 9 were transient, regularly traveling through the home ranges of other red foxes and between management units across the island.
- Average hourly movement rates of red foxes were highest overnight, 13–22 hours after sunrise.
- Within-home range habitat selection by red foxes differed among diel activity periods (split into a daytime period of low activity, 1–9 hours after sunrise; nighttime period of high activity, 13–22 hours after sunrise; and a transition period between encompassing all other hours).
  - Red foxes selected areas closer to wet sand, dry sand, and evergreen vegetation and farther from ORV roads and water than expected based on habitat availability, and showed no clear selection for or against development.
  - Red foxes selected areas closer to vegetation than expected based on availability during the daytime and transition hours but farther from vegetation than expected at night.

    - Avoidance of off-road vehicle (ORV) roads most strongly influenced selection patterns regardless of time of day.

Chapter 3: Using GPS location data to assess potential red fox responses to predator exclosures at piping plover nests

- Across all GPS-collared foxes, mean distances from each red fox's locations to nests were similar in the 48 hours before versus after exclosure setup, but differed following the first sign of pipping at nests and hatching.
    - Mean distance to nest decreased from 550m to 507m following the first sign of pipping, and increased from 773 to 794m following hatching.
    - Individual red fox responses varied widely. For example, 4 of the 9 red foxes included in our analyses appeared to respond to nest exclosure setup by using locations that were either on average closer to nests (n = 2 foxes) following setup or further from nests (n = 2 foxes).
- The proportions of red fox locations within 100-m buffers surrounding nests were similar before versus after exclosure setup, pipping, and hatching.
- Overall, red foxes in our study area did not appear to key in on nest exclosure setup, pipping, or hatching at the spatial scales considered in our comparisons.
    - However, red fox harassment at nest exclosures and depredation of nests were observed at Smith Point County Park in 2015 and 2018. Both exclosed and unexclosed nests in the park were depredated by red foxes in 2015; in 2018, only unexclosed were depredated by red foxes.

Chapter 4: Red fox dietary ecology in a semi-urban coastal ecosystem

- Red fox diets on Fire Island were highly varied, and included a wide range of natural and anthropogenic food items.
    - Orders Rodentia (rodents, 43% of scats), Coleoptera (beetles, 38%), and Decapoda (crabs and other crustaceans, 29%) occurred most frequently in scats examined (n = 293 scats).
    - Order Charadriiformes (shorebirds, including gulls, terns, and plovers) remains were found in 3% of scats examined.
    - Skates (Family Rajidae, 89% of dens with food items) and Atlantic surf clams (*Spisula solidissima*, 67%) were found outside the highest proportion of dens and made up 61% of all food items recorded at dens (n = 18 dens with food items, 278 total food items).
    - We found bird remains, primarily gulls (*Larus spp*.), outside of 44% of dens with food items.
    - We found anthropogenic items, primarily consisting of food wrappers and other packaging, in 16% of red fox scat samples and outside of 50% of dens with food items. These items made up 12% of all items recorded at dens.
- We did not find any clearly identifiable piping plover remains in red fox scats or outside of dens, but did find a pair of piping plover leg bands in a domestic cat scat (confirmed via genetic source species identification).
- Estimated litter sizes were positively correlated with the rate of fish accumulation at secondary dens (Spearman’s rank correlation coefficient: $\rho_3 = 0.95$, $P = 0.01$), indicating

that fish, which we suspect to be discarded angler bycatch, may represent an important food source for kits as they grow older.

MANAGEMENT IMPLICATIONS

- Our results suggest that that direct interactions between red foxes and piping plovers may be less frequent than previously believed, but red foxes may have a disproportionate impact at some sites and in some years.
    - Considered alongside the findings of concurrent piping plover monitoring (Bellman 2019, Robinson 2020, Walker 2020), these findings suggest that red fox predation is only one of many different factors influencing piping plover population growth in the study area; habitat availability appears to be a key factor in piping plover population growth on the island as well.
    - There is some evidence that red fox abundance may indirectly influence piping plover population growth. For example, chick survival was higher following red fox population declines due to mange outbreaks (Robinson 2020).
- When the observed sarcoptic mange outbreaks are considered as a proxy for what may happen under intensive lethal removal of red foxes to manage predation of threatened and endangered shorebirds, our results suggest that such efforts may not be effective in reducing the spatial distribution of red foxes or eliminating red foxes from nesting areas unless complete eradication can be achieved across the island.
    - Red fox occupancy remained high at each site in all years that foxes were present, despite sharp declines in minimum red fox abundance and density, suggesting that

  fewer foxes does not necessarily translate to changes in red fox presence across the landscape.
  - Nearly a third of GPS-collared red foxes were transient, regularly traveling between study sites and across long distances, suggesting high capacity for dispersal should an occupied territory become vacant.
- Strategic vegetation management in and around known piping plover nesting areas could reduce daytime resting areas and hunting concealment for red foxes while improving relative suitability for use by piping plovers.
- We recommend continued use of nest exclosures in the study area, based on the lack of clear evidence of red fox responses to setup, pipping, or hatching.
  - We encourage managers to take advantage of existing decision-making tools (e.g., Darrah et al. 2020) to continually reassess the effectiveness of nest exclosures in improving population growth in light of potential changes in nest predation and adult survival rates across years.
- We recommend that future predator monitoring activities consider all potential predators on the island, rather than focusing on a single predator species.
- We recommend that future predator management activities consider the potential impacts of free-ranging cats, given the observation of piping plover remains in a domestic cat scat. We recommend continued efforts to reduce public feeding of red foxes and encourage visitors and residents to dispose of food waste in secure containers.
  - Although anthropogenic food waste was not clearly correlated with higher red fox reproductive success, these items made up a non-trivial portion of red fox diets on Fire Island during the study period.

    - Waste management programs should also encourage proper disposal of angler discards, as fish remains made up the majority of food items found outside of dens and the amount of fish remains found at a den was positively correlated with red fox litter size.

FUTURE RESEARCH NEEDS

In addition to the above management recommendations, we recommend further research in the following areas:

1. Red fox population recovery following mange outbreaks
    - We recommend continued monitoring of red foxes on Fire Island to assess population recovery following mange outbreaks, as this monitoring may provide insight into how long it may take for a red fox population to recover from a sharp reduction in numbers (similar to what may be achieved through intensive lethal removal efforts) in a relatively closed system.
    - We recommend that continued monitoring of red foxes on Fire Island include den monitoring, particularly in the early years of population recovery, to determine whether compensatory reproduction occurs.
2. Changes in red fox space use following mange outbreaks
    - Our remote camera results from Chapter 1 suggest that as population density in the study area declined, remaining red foxes expanded their space use to include previously occupied areas, resulting in consistently high occupancy despite mange-related die-offs. Trap success, however, decreased with population density, suggesting that red foxes may have been using the area less intensely. Further

research is needed to determine whether this is the case, and how intensity of space use by red foxes might correspond to piping plover predation risk.

3. Red fox behavioral responses to nest exclosures
    - Further research should combine GPS collar data with nest cameras to take advantage of multiple data sources.
4. Probability of detection of piping plover consumption
    - Non-detection of piping plover remains in red fox scats does not necessarily mean that piping plovers were not consumed; it is possible that non-detection of scats during transects, or non-detection of or piping plover remains in collected scats may have influenced our results. Further investigation into scat detection rates and detection of avian remains in scats may help quantify the probability that piping plovers were consumed but not detected in our dietary analyses.
5. Effects of anthropogenic resources on red fox ecology
    - Our comparisons in Chapter 4 examined the relationships between anthropogenic resource use and litter sizes, and indicated that angler discards may be contributing to increased reproductive success. However, more information is needed to determine what proportion of fish observed at dens are obtained from angler discards vs. natural wash-up.
    - Although we did not observe a correlation between anthropogenic food waste at dens and litter size, it is possible that these items may be influencing other aspects of fox ecology in our study area, such as survival rates or population density. If so, these resources may be indirectly influencing red fox interactions with piping plovers and other species of concern. We recommend further research into the relationship

between anthropogenic food waste availability and use, and red fox population parameters.

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