



# Responses of a federally threatened shorebird to trophic downgrading and expansion of domestic cats (*Felis catus*)

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**Abstract** Along U.S. Atlantic and Gulf Coast barrier islands, red foxes (*Vulpes vulpes*) are top predators that are thought to impact smaller mesopredators and depredate beach-nesting birds. Starting in 2015, sarcoptic mange epizootics among red foxes led to their eventual temporary extirpation from most of Fire Island, NY, USA. We monitored the subsequent changes to the mammalian predator community on this barrier island and explored the impacts to piping plovers (*Charadrius melodus*), a federally threatened shorebird. We deployed trail cameras and quantified detection rates of four common shorebird predators (red foxes, northern raccoons *Procyon lotor*, Virginia

opossums *Didelphis virginiana*, and invasive domestic cats *Felis catus*), and tested for effects of predator activity and density on piping plover nest and brood survival. Following the loss of red foxes, northern raccoon and Virginia opossum activity remained relatively unchanged, while cat activity increased. The cat population grew from 14 to 42 individuals across the three study areas, and cats later became the most frequently detected mammalian predator. The loss of red foxes was associated with increased plover nest survival ( $\beta \pm \text{SD} = 1.08 \pm 0.55$ ), though the increase of cats in later years was associated with a strong, negative decline in nest survival ( $\beta \pm \text{SD} = -3.08 \pm 1.28$ ). Plover brood interval survival was negatively correlated with cat density ( $\beta \pm \text{SD} = -0.50 \pm 0.14$ ) but not with red foxes. We underscore the importance of monitoring invasive predators during periods

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of trophic downgrading, which may have delayed impacts to native fauna.

**Keywords** Barrier island · *Charadrius melodus* · Domestic cat · *Felis catus* · Invasive island predator · Piping plover

## Introduction

Globally, top predators are in decline (Estes et al. 2011; Ripple et al. 2014). When top predators are extirpated, the loss of top-down consumptive (i.e. predation) and non-consumptive effects (e.g., perceived predation risk, competition) can reverberate through food webs (Ripple et al. 2016). Following the disappearance of a top predator, populations of smaller predators within the community may experience population growth, and the resulting change in predatory pressures can lead to prey population declines (Soulé et al. 1988; Crooks and Soulé 1999). In extreme cases, increased predation by multiple competing mesopredators may result in species extirpations (Crooks and Soulé 1999).

Predator–prey interactions are especially complex in island systems with invasive species (Courchamp et al. 1999). Invasive mammals are one of the greatest threats to insular biodiversity (Blackburn et al. 2004; Medina et al. 2011; Doherty et al. 2016) and they often are targets for predator control or eradication programs (Jones et al. 2016; Spatz et al. 2022). However, asymmetric management, where one species in a multi-predator system is the focus of predator control, can lead to unintended consequences (Zavaleta et al. 2001). For example, predator control programs solely focused on managing a top predator may enable smaller mesopredators to expand their dietary niche (Rayner et al. 2007; Stantial et al. 2021), while the reduction of a mesopredator as prey may lead to increased predation pressures elsewhere in the system (Murphy and Bradfield 1992). Thus, it is vital to understand the complex nature of predator guilds for holistic wildlife management (Zavaleta et al. 2001; Doherty and Ritchie 2017).

Barrier islands provide important foraging and nesting habitat ground-nesting birds, including migratory shorebirds. In these systems, predator control commonly is used in shorebird management (Hunt et al. 2019). Wild canines, such as the red fox (*Vulpes*

*vulpes*), sometimes are top predators in barrier island communities and are thought to contribute to the regulation of bird and mammal populations (Patterson et al. 1991; Radford et al. 2018; Hunt et al. 2019; Stantial et al. 2021; Robinson et al. 2024). There is some evidence that red foxes suppress smaller predators (e.g., Stantial et al. 2021), including domestic cats (*Felis catus*; Rees et al. 2023). In areas where red foxes and feral cats co-occur, domestic cats apparently avoid core parts of red fox territories (Molsher 1999; Glen and Dickman 2005).

From 2015–2018, the red fox population at Fire Island, NY experienced a multi-year epizootic of sarcoptic mange (Black 2021; Wails et al. 2024). Sarcoptic mange is a parasitic disease that creates high mortality rates among wild canids (Niedringhaus et al. 2019) and red foxes were subsequently extirpated from part of this barrier island system (Black 2021; Wails et al. 2024). Here, we evaluate evidence that the reduction of red foxes, which were the top predator at Fire Island prior to the mange-caused extirpation (Black 2021), was associated with a subsequent change in the mammalian predator community, which affected a federally threatened shorebird (Robinson et al. 2024). We first tested whether the mange-related decline in red foxes resulted in a release within the mesopredator community by comparing the relative activity rates of four mammalian shorebird predators using data from a trail camera study. We then focused on the dynamics between red foxes and domestic cats, as cats were the only predator with a consistent increase in their activity across all study areas. We identified cats and estimated their abundance and survival before and after the extirpation of red foxes. We then contrasted the demographic association of the mange-induced changes of red foxes and cats on the nest and brood survival rates of piping plovers (*Charadrius melodus*) while controlling for density-dependence (Catlin et al. 2015; Robinson et al. 2024).

## Methods

### Study system and fieldwork

Fire Island, NY, USA (40°39' N, 73°05' W) is a c. 2,360 ha barrier island off the southern shore of Long Island, NY, and consists of residential villages, county and state parks, and a federally

designated wilderness area (Fig. 1). In October 2012, Hurricane Sandy breached Fire Island and separated a 10-km eastern portion from the 40-km western portion (Hapke et al. 2013). This breach was left to undergo accretion and erosion processes, likely preventing movements of terrestrial mammals between the eastern and western portions of the island (Black 2021) until the breach closed in November 2022.

The mammal community on Fire Island is a mix of native, naturalized, and invasive species (Connor 1971; McElroy et al. 2009). The most abundant shorebird predators include red foxes, northern raccoons (*Procyon lotor*), Virginia opossums (*Didelphis virginiana*), and domestic cats (Patterson et al. 1991; Houghton 2005; Doherty and Heath 2011; Black 2021; Stantial et al. 2021). Red foxes, northern raccoons, and Virginia opossums have native ranges within eastern North America, though there is some debate whether the arrivals of red foxes and Virginia opossums to Long Island and the nearby barrier islands resulted from natural range expansion or introductions (cf. Connor 1971; Statham et al. 2012). Red foxes on Fire Island are likely a naturalized population, as individuals have a mixed background of wild native and fur trade ancestry (Black 2021). Domestic cats are an invasive species (Medina et al. 2011) and the population is a mix of purposefully released individuals, free-roaming

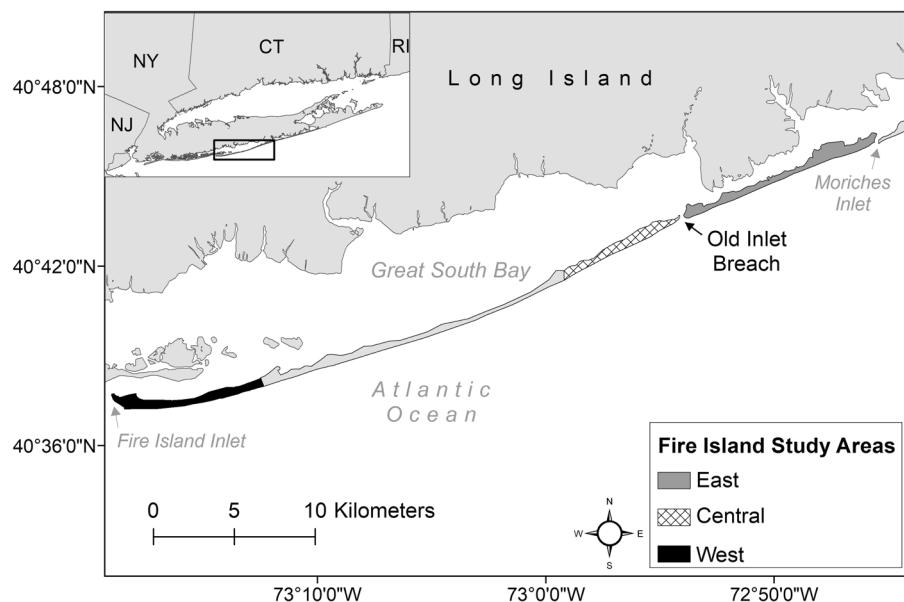
pets, and escapees from the interior villages on Fire Island and nearby Long Island.

Fire Island supports an important breeding population of piping plovers (Weithman et al. 2019; Robinson et al. 2020). In 1986, the Atlantic coast piping plover population was listed as threatened under the U.S. Endangered Species Act following range-wide population declines (USFWS 1985, 1996). Reducing predation is a common management goal for piping plover conservation (USFWS 1996, 2020; Hunt et al. 2019; Robinson et al. 2024). We monitored the mammalian predator community and nesting piping plovers in three focal study areas consisting of county, state, and federal parks, including the Otis Pike Fire Island High Dune Wilderness managed by the National Park Service (Walker et al. 2019; Robinson et al. 2020; Black 2021) (Fig. 1).

### Predator monitoring

We used automated trail cameras to facilitate monitoring of the predator community. From Sept–Mar of 2015–2018, we deployed 96–100 unbaited camera stations across the entire study site (typically 28–40 camera stations per study area) with camera stations placed c.  $300 \pm 50$  m apart (Black 2021). Each camera station consisted of two motion-triggered cameras (Moultrie M880c and M880 Gen 2; Moultrie Feeders, Calera, AL) attached to T-posts and placed

**Fig. 1** Study areas on Fire Island, NY, USA monitored 2013–2023. Predator and shorebird monitoring occurred in three areas (from east to west): (1) east of the Old Inlet breach (dark gray), (2) central Fire Island just west of the Old Inlet breach (hashed), and (3) west Fire Island (black)



1–3 m apart along opposite sides of game trails or clearings to photograph both sides of an animal. We programmed cameras to take three sequential photos when triggered by motion with a 5 s delay between triggers.

To inform estimates of red fox abundance, we conducted transect surveys six times per year 2015–2019 (three in spring–summer, three in autumn–winter; Black 2021) and 1–2 times per year (summer only) in 2021 and 2022. We established 96 north–south transects that were spaced c. 300 m apart and overlapped camera station locations. During transect surveys, we recorded observations of predators, predator evidence (tracks, scat, den locations), and signs of breeding (e.g., variation in track and scat sizes at dens, recent prey items present at dens, observations of red fox kits; Black 2021). From 2015–2018, we derived estimates of red fox abundance by monitoring marked individuals (GPS-collars or ear tags) or were otherwise distinguishable (e.g., unmarked adults within breeding groups) by Black (2021). In 2019–2022, we estimated red fox abundance from transect surveys, opportunistic sightings, and reports from land managers, adhering to standardized sampling protocols from Black (2021).

#### Plover monitoring

To assess the demography of nesting piping plovers (hereafter, ‘plovers’), we monitored plovers in concert with local land managers from April–August 2013–2019 and 2021–2023. We searched for plover nests by surveying potential nesting habitat and observing adult plover behavior. We estimated the date of nest initiation by backdating 1.5 days per egg for partial clutches (Robinson et al. 2020) or by floating eggs to determine the number of days of incubation if the nest was found at full clutch (Westerskov 1950). We assumed 28 days for incubation after clutch completion (Elliott-Smith and Haig 2004). Land managers determined whether a nest received an exclosure (i.e. metal cages that physically prevent medium to large predators from accessing nests; Melvin et al. 1992; Black et al. 2023). We checked nests at regular intervals and we noted evidence of predator activity (e.g., tracks). We considered nests to be successful when  $\geq 1$  egg hatched.

We attempted to capture and band all plover chicks from monitored nests, issuing either a unique

combination of four Darvic color bands to the tibiotarsus or a uniquely coded alphanumeric Darvic flag (Interrex, Łódź, Poland) with an engraved Darvic color band on the opposite tibiotarsus. We then surveyed for plover broods approximately every 1–7 days until chicks reached 30 days old. We considered chicks fledged at 25 days of age (Hunt et al. 2013; Catlin et al. 2015; Robinson et al. 2024).

#### Aerial imagery

To account for spatial heterogeneity in plover nest site selection within estimates of plover nesting density (Walker et al. 2019; Dorsey 2023), we quantified the area of nesting habitat within 20 discrete segments of beach ( $\text{mean} \pm \text{SE} = 15.2 \pm 0.6$  ha) that were relatively homogenous in geomorphological characteristics (Wails et al. 2023). We collected high-resolution (15-cm) imagery and LiDAR elevation data (NAD 1983 State Plane NY Long Island, FIPS 3104 [feet]; Axis Geospatial, Easton, MD) in April for 2013–2023. In ArcMap (vers. 10.3–10.8; Esri Inc., Redlands, CA, USA) and ArcGIS Pro (ver. 3.1.3; Esri Inc.), we projected all spatial layers to WGS 1984 and calculated the annual total land area (ha) of each study area. We used supervised classification of land cover to calculate the area of contiguous dry sand patches  $\geq 1$  m<sup>2</sup> above the mean high tide line (Walker et al. 2019; Robinson et al. 2021).

#### Statistical analyses

##### *Assessing predator community changes*

We quantified detection rates of red foxes, northern raccoons, Virginia opossums, and cats per 100 trap nights using independent detections of each species. We considered detections to be independent when individuals of the same species were detected  $> 30$  min apart (Brook et al. 2012; Rovero and Zimmermann 2016). We then tested for changes in the predator community from 2015–2018 by analyzing the detection rates of the four predators using generalized linear mixed-effects models with a negative binomial error distribution via the R package *glmmTMB* (Brooks et al. 2017) in the statistical computing environment R, ver. 4.3.1 (R Core Team 2023). We used the frequency (count) of independent detections per camera station as the dependent variable and

included an offset of trap nights ( $\ln(\text{trap nights}/100)$ ) in all candidate models to standardize frequencies. We included predator species and year relative to the sarcoptic mange epizootics (0 = first year sarcoptic mange observed in the study area) as independent variables. The global model included both additive terms and their interaction. Our candidate model set included a null model (intercept-only), two singular term models, a model with species and year relative to the sarcoptic mange epizootics as additive effects, and the global model. Because we deployed camera stations at approximately the same locations in multiple years but in slightly different combinations, we included study area and camera station location as nested random effects in all candidate models. We checked for collinearity of covariates and excluded combinations when  $|r| \geq 0.7$ . We checked all standard model assumptions (e.g., distribution of residuals), including tests for temporal and spatial autocorrelation, via the R package *DHARMa* (Hartig 2022). We ranked candidate models via Akaike's information criterion (Akaike 1974) corrected for sample size ( $AIC_c$ ; Hurvich and Tsai 1989) and used  $\Delta AIC_c$  and  $AIC_c$  weights ( $\omega_i$ ) to evaluate model support (Burnham and Anderson 2002; Johnson and Omland 2004).

#### Identifying cats and estimating their abundance and survival

We identified cats photographed at camera stations during the 2015–2018 camera study to estimate their minimum population size. We did not attempt to estimate the abundance of northern raccoons or Virginia opossums, as their activity rates were largely unaffected by the change in red fox abundance and activity. To identify individual cats, we examined distinct pelage patterns on the head and face, body, and legs, and recorded any other characteristic features (e.g., 'ear tipping,' wherein the tip of one ear is surgically removed during trap-neuter-return programs; Dalrymple et al. 2022). We then compared whole body images of cats to those where only part of a cat was visible to match visible pelage patterns. Each cat identification was reviewed by two individuals to check for misidentifications.

We estimated apparent survival ( $\phi$ ) of adult cats using data from the 2015–2018 camera study, using a Cormack-Jolly-Seber model (Lebreton et al. 1992) via the R package *marked* (Laake et al. 2023). We

tested for effects of time, subpopulation (i.e. study area), and their interaction on apparent survival; we included time and subpopulation but excluded their interaction on detection probability ( $p$ ). We modeled all combinations of structures, including constant rates, resulting in a candidate set of 12 models. We ranked models by Akaike's information criterion (Akaike 1974) and used  $\Delta AIC$  and AIC weights ( $\omega_i$ ) to evaluate model support (Burnham and Anderson 2002; Johnson and Omland 2004).

We estimated cat abundance in 2019–2022 after the camera study concluded and when red foxes were largely extirpated. We estimated subpopulation size of cats in each of the three study areas using a density-dependent ordinary differential equation for logistic growth:

$$\frac{dN}{dt} = rN(1 - \alpha N)$$

where  $N$  is the population starting size,  $r$  is the per capita growth rate, and  $\alpha$  is the per capita effect of an individual on the growth rate, expressed as:

$$\alpha = \frac{1}{K}$$

where  $K$  is the carrying capacity. We used the minimum subpopulation size of cats from 2015 in each of the three study areas as the starting subpopulation size (i.e. year 0) and used the rate of change in identifiable cats observed during the 2015–2018 camera study as the subpopulation growth rate. We assumed a carrying capacity of 0.079 cats/ha, which was generated from studies of feral cats on islands with no or small human populations by Flockhart and Coe (2018). Because barrier islands can vary substantially between years, we used the average land area for all years prior to the Old Inlet breach closing (2013–2022) to estimate carrying capacity for each study area. We then used the *ode* function via the R package *deSolve* (Soetaert et al. 2010) to numerically solve the differential equation.

#### Quantifying predator impacts on plover demography

We used a logistic exposure model (Rotella et al. 2004; Shaffer 2004; Robinson et al. 2020) to test for correlates of ecological covariates on plover nest survival in 2013–2023. Covariates included presence of



predator exposure (0=not exposed, 1=exposed), nest age, ordinal date of nest observation, clutch size, nesting density (pairs/ha of nesting habitat), timing of the sarcoptic mange epizootics (i.e. number of months before or after mange signs first observed in the study area where 0=first month of sarcoptic mange), year, and presence of predator activity at the nest (0=no activity detected, 1=tracks or other evidence present) for red foxes and cats separately. We included interactions between year and predator activity of red foxes and cats. We included a random effect to account for repeat observations of the same nest. We then calculated age-specific daily survival rate as:

$$DSR_i = \frac{e^{\beta_0} + \sum_j \beta_j \chi_{ji}}{1 + e^{\beta_0 + \sum_j \beta_j \chi_{ji}}}$$

where  $i$  represents day,  $j$  is the  $j$ th covariate, and  $\beta_j$  is the coefficient of covariate  $j$  (Rotella et al. 2004). We then calculate annual nest survival as the product of year- and age-specific estimates of DSR (Weiser 2021) for ages 1–34 (i.e. the typical exposure period for a four-egg plover clutch; Catlin et al. 2015; Robinson et al. 2020).

We quantified plover brood survival ( $\phi$ ) to fledging using a modified Dail-Madsen model (Dail and Madsen 2011), which is a Bayesian implementation of the Lukacs young survival from marked adults model (Lukacs et al. 2004), as described by Robinson et al. (2020). We estimated survival over a 25-day period using 5-day detection intervals. We developed a model to test whether interval survival was correlated with ordinal hatch date, nesting density (pairs/ha plover nesting habitat), observed red fox density (individuals/ha total land area), and projected cat density (individuals/ha total land area) using estimates from the ordinary differential equation for logistic growth. In this analysis, we limited data to 2016–2022 to coincide with years of red fox observations and projected cat estimates. We calculated interval survival rate as:

$$\text{logit}(\phi_{w,v}) = \phi_\mu + \beta_{t,w,v} X_{t,w,v}$$

where  $\phi_{w,v}$  is the survival probability for brood  $w$  and detection interval  $v$ , and  $\beta_{t,w,v}$  is the coefficient of brood, year, or occasion-specific covariates. We used the product of the four 5-day intervals as brood survival.

We used Bayesian Markov chain Monte Carlo (MCMC) analysis with JAGS (Plummer 2003) via the R package *jagsUI* (Kellner and Meredith 2021) for both plover nest and brood survival. We scaled all continuous covariates by two standard deviations to facilitate comparison of parameter estimates between continuous and unscaled binary covariates (Gelman 2008). We used normally distributed vague priors ( $\mu=0$ ,  $\tau=0.001$ ) for all estimated parameters and a uniform prior for random effects. For each analysis, we implemented 3 MCMC chains with 100,000 iterations, burn-in and adapt periods of 25,000 iterations each, and a thinning rate of 2 (Robinson et al. 2020), resulting in posterior samples of 112,500. We assessed model diagnostics by visually inspecting chains and checking for convergence ( $\hat{R} \leq 1.05$ ; Gelman and Rubin 1992). We report estimates using the mean of the posterior distribution, the corresponding 85% Bayesian credible intervals (CRIs; Arnold 2010), and  $f$ , which represents the proportion of the posterior distribution that is above or below 0. We inferred parameter importance when the 85% CRIs did not overlap 0 (Payton et al. 2003).

## Results

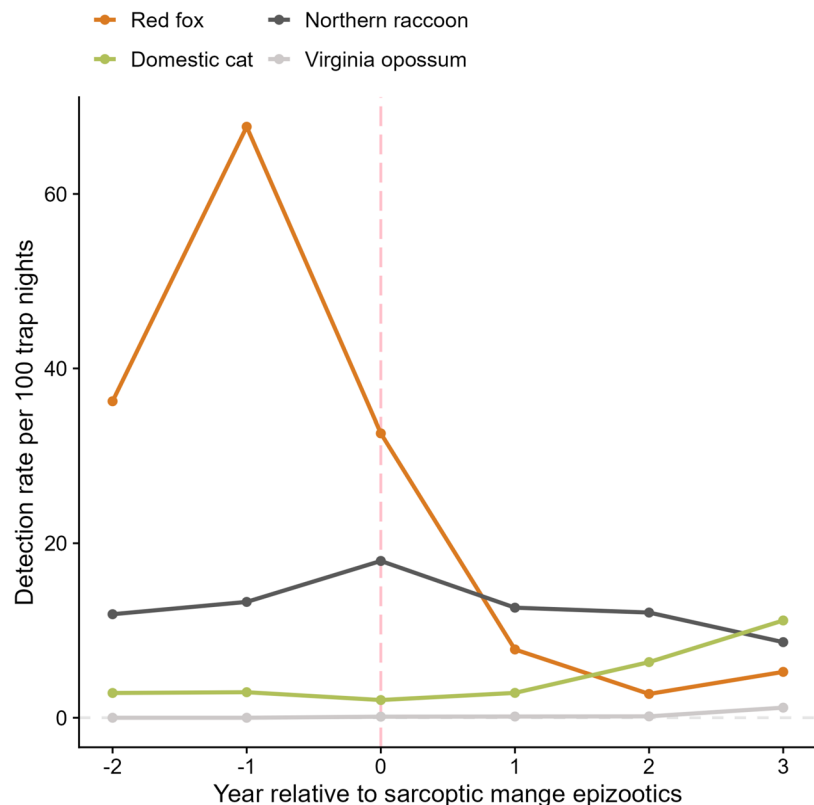
### Predator community changes

We recorded 42,361 total independent detections of wildlife at camera stations, with 13,734 detections (32.4%) composed of the four mammalian predators of interest (red foxes=19.4% of all wildlife detections, northern raccoons=10.3% of all wildlife detections, cats=2.6% of all wildlife detections, Virginia opossums=0.1% of all wildlife detections; Table 1). The global model was the top-ranked model in our candidate set and received >99.9% of model weight (Table S1). Before the sarcoptic mange epizootics, red foxes were the most frequently detected predator (Fig. 2). Shortly after the epizootics were first observed, detection rates of northern raccoons briefly exceeded that of red foxes, though remained fairly stable through the camera study. Cat detection rates increased slowly throughout the camera study and exceeded that of the other predators three years post-mange. Virginia opossums seldom were detected during the camera study.

**Table 1** Detection rates (detections/100 trap nights) of the four mammalian predators (red foxes *Vulpes vulpes*, domestic cats *Felis catus*, northern raccoons *Procyon lotor*, and Virginia opossums *Didelphis virginiana*) on Fire Island, NY, USA during the 2015–2018 camera trapping study

Camera trapping session	Dates of operation	Camera stations	Trap nights	Total detections	Red fox	Domestic cat	Northern raccoon	Virginia opossum
2015/2016	26 Oct–04 Feb	100	4,794	8,642	2,559 (29.6%)	202 (2.3%)	904 (10.5%)	0 (0.0%)
2016/2017	04 Oct–30 Jan	99	5,076	10,587	2,962 (28.0%)	190 (1.8%)	1,131 (10.7%)	4 (<0.1%)
2017/2018	29 Sep–16 Mar	96	6,886	13,882	2,354 (16.9%)	190 (1.4%)	1,552 (11.2%)	17 (0.1%)
2018/2019	26 Sep–23 Jan	96	5,493	9,250	338 (3.7%)	515 (5.6%)	789 (8.5%)	29 (0.3%)
Total			22,271	42,361	8,211 (19.4%)	1,097 (2.6%)	4,376 (10.3%)	50 (0.1%)

**Fig. 2** Detection rates (per 100 trap nights) of the four mammalian predators (red foxes *Vulpes vulpes*, northern raccoons *Procyon lotor*, Virginia opossums *Didelphis virginiana*, and domestic cats *Felis catus*) on Fire Island, NY, USA in 2015–2018. Detection rates are presented relative to the first year of the sarcoptic mange epizootic in the study area; negative values indicate years prior to observations of sarcoptic mange, and positive values indicate years after sarcoptic mange was detected



Red fox abundance across the three study areas was greatest in 2016 (min. 35 individuals/study area) and declined through 2017 (min. 29 individuals/study area) and 2018 (min. 5 individuals/study area; Table 2). We detected intermittent presence

of red foxes from 2019–2022 (0–2 individuals/study area annually), and there was no evidence of red foxes breeding within the three study areas since the sarcoptic mange epizootics.

**Table 2** Predator abundances of red foxes (*Vulpes vulpes*) and domestic cats (*Felis catus*) within the three study areas on Fire Island, NY, USA in 2015–2022. Estimates of red foxes 2015–2018 are from Black (2021)

Study area	Year	Red foxes				Domestic cats
		Newly marked foxes	Previously marked and unmarked foxes	Active breeding dens	Minimum foxes	Minimum cats
East	2015	4	–	–	–	4
	2016	0	0	4	0	6
	2017	0	1	4	1	12
	2018	0	1	0	1	15
	2019	0	0	0	0	–
	2020	0	0	0	0	–
	2021	0	0	0	0	–
	2022	0	1	0	1	–
Central	2015	3	–	–	–	3
	2016	6	29	4	35	2
	2017	7	6	2	13	4
	2018	0	1	0	1	7
	2019	0	0	0	0	–
	2020	0	0	0	0	–
	2021	0	2	0	2	–
	2022	0	1	0	1	–
West	2015	9	–	–	–	7
	2016	6	19	0	25	6
	2017	10	9	0	29	11
	2018	3	2	0	5	20
	2019	0	0	0	0	–
	2020	0	0	0	0	–
	2021	0	1	0	1	–
	2022	0	1	0	1	–

### Cat abundance and survival

We captured 3,125 images of cats, and 2,852 (91.3%) of those images were of sufficient quality to identify individuals. We identified 59 different cats during the 2015–2018 camera study, and there was evidence of breeding (visibly pregnant and lactating females). During the 2015 and 2016 camera study periods, we identified 14 cats across the three study areas, increasing to 27 individuals in 2017, and 42 individuals in 2018, when the camera study concluded (Table 2). Cats were photographed at 65 of the 100 camera stations (2015=23 stations [23.0% of stations], 2016=14 stations [14.1% of stations], 2017=33 stations [34.4% of stations], 2018=56 stations [58.3% of stations]). There was no evidence that cats moved between the three study areas.

Apparent survival and detection rates of adult cats did not differ between study areas or with time (Table S2). Annual apparent survival of adult cats was high ( $\phi \pm SE = 0.78 \pm 0.06$ ) and our annual detection rate was similarly high ( $p \pm SE = 0.90 \pm 0.06$ ). Estimates of cat carrying capacity ranged 30.3–47.7 individuals per study area, and subpopulations within each study area were predicted to reach carrying capacity within 10–20 years (Fig. 3).

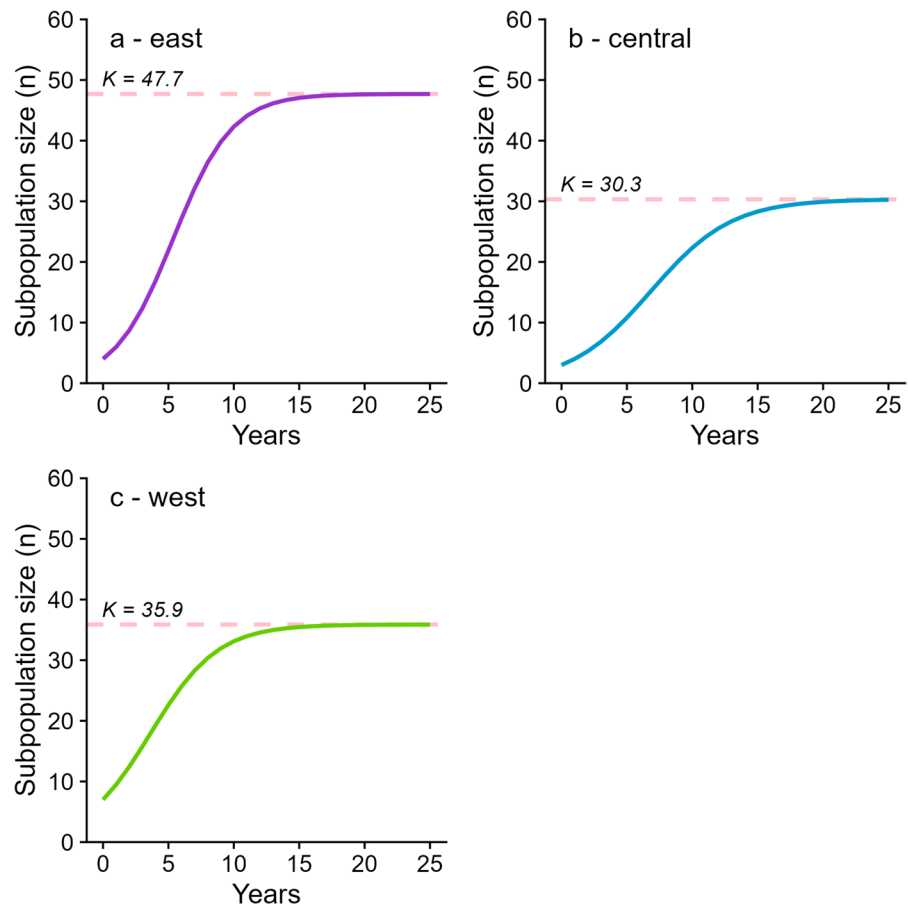
### Predator impacts on plover demography

#### Plover nest survival

From May–July 2013–2023, we located and monitored 649 plover nests in collaboration with land managers. The average number of visits to monitored



**Fig. 3** Projected subpopulation growth of domestic cats (*Felis catus*), starting from 2015 (year 0), for the **a** east, **b** central, and **c** west study areas on Fire Island, NY, USA. Carrying capacity ( $K$ , equivalent to 0.079 cats/ha; Flockhart and Coe 2018) is shown

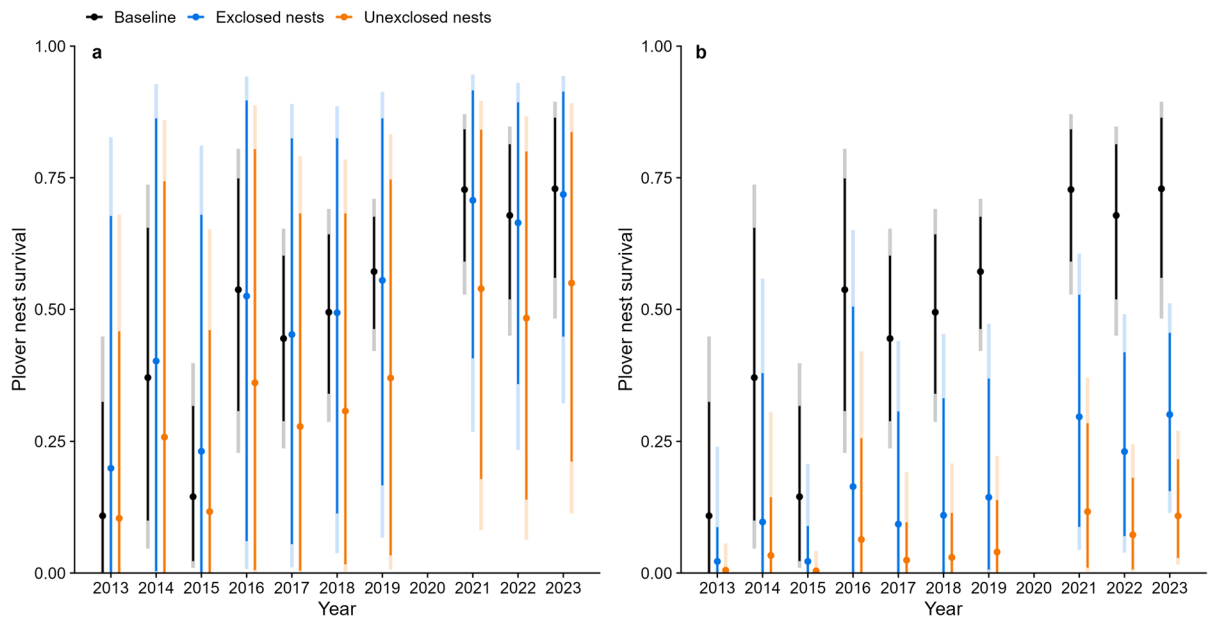


nest was 9.43 (SE =  $\pm 0.24$ , range = 2–31 visits) with an average interval of 2.73 days (SE =  $\pm 0.03$ , range = 1–35,  $n = 5,507$  intervals). Plover clutch size averaged 3.65 eggs (SE  $\pm 0.03$ , range = 1–6). More than half of monitored nests hatched at least one egg (407 of 649 nests [62.7%] hatched at least one egg, range = 24.3–79.4% annually). Suspected causes of nest failure varied annually and included abandonment ( $n = 98$ , 40.5% of failed nests; Fig. S1a), predation ( $n = 87$ , 36.0% of failed nests; Fig. S1b), vandalism and unknown causes ( $n = 37$ , 15.3% of failed nests), and weather events ( $n = 20$ , 8.3% of failed nests).

Nest survival increased with the presence of a nest enclosure ( $\beta = 0.90$ , SD = 0.17, 85% CRI = 0.65–1.14,  $f = 1.00$ ) and increased with clutch size ( $\beta = 0.51$ , SD = 0.14, 85% CRI = 0.30–0.71,  $f = 1.00$ ), but declined with plover nesting density ( $\beta = -0.44$ , SD = 0.18, 85% CRI = -0.70 to -0.19,  $f = 0.99$ ) and nest age ( $\beta = -0.51$ , SD = 0.20, 85%

CRI = -0.80 to -0.23,  $f > 0.99$ ; Fig. S2a). There was no effect of date on nest survival ( $\beta = -0.06$ , SD = 0.15, 85% CRI = -0.28–0.15,  $f = 0.66$ ). Plover nest survival was positively associated with red foxes following the mange epizootics (red fox activity  $\times$  mange  $\beta = 1.08$ , SD = 0.55, 85% CRI = 0.31–1.89,  $f = 0.98$ ) but negatively associated with cats (cat activity  $\times$  mange  $\beta = -3.08$ , SD = 1.28, 85% CRI = -4.98 to -1.33,  $f > 0.99$ ).

Nest survival typically was high in the absence of mammalian predator activity (baseline, Fig. 4). When red fox activity was observed, nest survival probabilities for exclosed and unexclosed nests did not differ from the baseline nest survival, as the 85% credible intervals for all three scenarios overlapped (Fig. 4a). Cat activity at plover nests was associated with an apparent reduction in nest survival at exclosed and unexclosed nests from 2018–2023 (Fig. 4b).



**Fig. 4** Piping plover (*Charadrius melodus*) nest survival estimates on Fire Island, NY, USA in 2013–2023. Survival estimates are from a logistic exposure model while other covariates are held at the mean. Baseline nest survival (i.e. annual survival in the absence of predators and without nest exclo-

tures) is shown in black. Annual nest survival for exclosed (blue) and unexclosed (orange) nests when **a** red foxes (*Vulpes vulpes*) are present and **b** when domestic cats (*Felis catus*) are present. Solid error bars depict 85% credible intervals and opaque error bars depict 95% credible intervals

### Plover brood survival

From May–August 2016–2022, we located and monitored 256 plover broods. Plover brood size at hatch averaged 3.38 chicks ( $SE = \pm 0.05$ , range = 1–4). On average, 1.85 chicks per brood fledged annually ( $SE = \pm 0.09$ , range = 0–4, 194 of 256 broods [75.8%] fledged at least one chick).

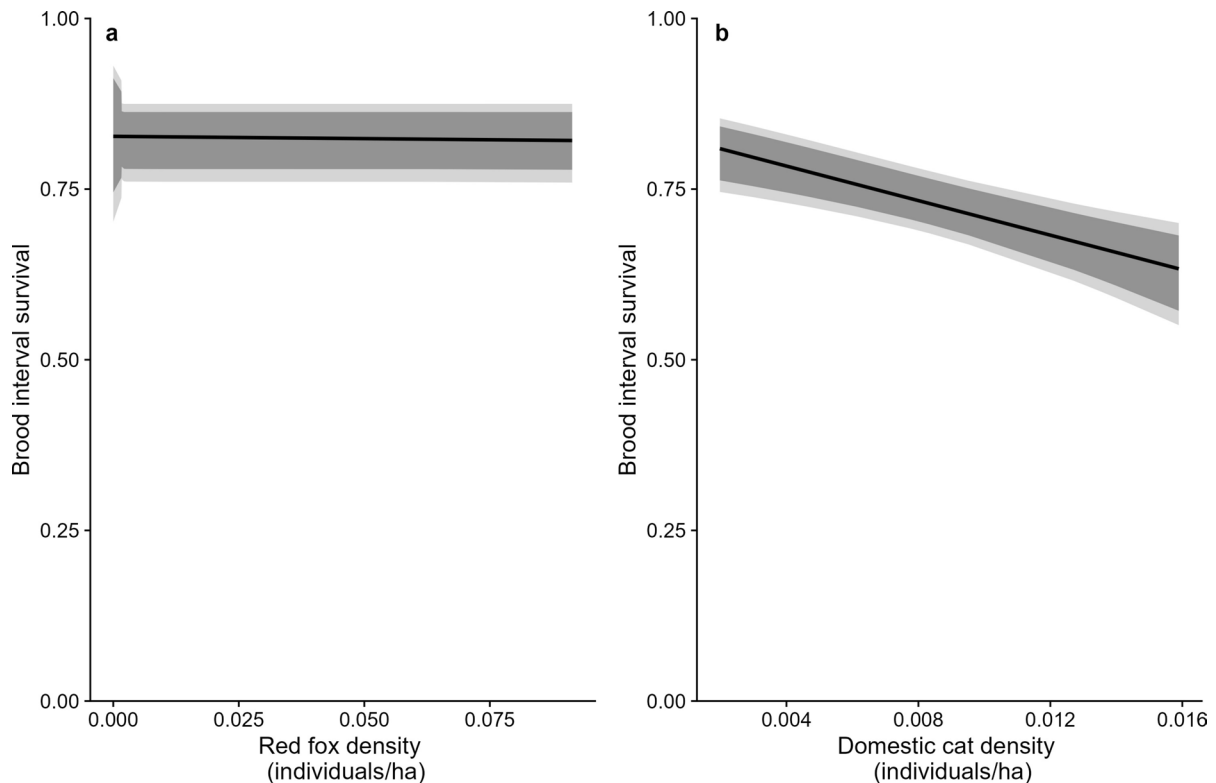
Brood interval survival increased with chick age ( $\beta = 0.35$ ,  $SD = 0.04$ , 85% CRI = 0.29–0.42,  $f = 1.00$ ), but decreased with later hatching dates ( $\beta = -0.60$ ,  $SD = 0.13$ , 85% CRI = -0.78 to -0.41,  $f = 1.00$ ) and high plover nesting density ( $\beta = -0.40$ ,  $SD = 0.14$ , 85% CRI = -0.60 to -0.21,  $f > 0.99$ ; Fig. S2b). Brood interval survival was unaffected by red fox density ( $\beta = 0.05$ ,  $SD = 0.14$ , 85% CRI = -0.15–0.25,  $f = 0.62$ ; Fig. S2b) and ranged from 0.84 (85% CRI = 0.75–0.91) when red foxes were absent to 0.82 (85% CRI = 0.78–0.86) at the greatest red fox density (0.091 red foxes/ha; Fig. 5a). Brood interval survival declined with projected cat density ( $\beta = -0.50$ ,  $SD = 0.14$ , 85% CRI = -0.70 to -0.30,  $f > 0.99$ ; Fig. S2b) and was predicted to decline approximately 5% for every 7–8 additional cats in a subpopulation

(approximating a 0.004 increase in cat density; Fig. 5b). At the lowest cat density (0.002 cats/ha), we estimate brood interval survival was 0.80 (85% CRI = 0.76–0.84). Brood interval survival was 0.63 (85% CRI = 0.57–0.68) when cat density reached 0.016 cats/ha.

### Discussion

Through our monitoring set up, we detected an increase in the cat population at Fire Island that occurred following a multi-year sarcoptic mange epizootic among red foxes. In the absence (or near-absence) of red foxes, plover nest and brood survival rates were negatively correlated with the activity and projected population density of cats. We did not find negative correlates of red foxes on plover survival.

Prior to their extirpation, red foxes likely reduced cat activity in plover nesting areas, though it remains unclear whether red foxes depressed cat subpopulations. Although red foxes may depredate cats (Glen and Dickman 2005), cats were not detected in analyses of Fire Island red fox diet in 2011–2012 (Peterson



**Fig. 5** Piping plover (*Charadrius melodus*) brood interval survival in relation to **a** observed red fox (*Vulpes vulpes*) density and **b** projected domestic cat (*Felis catus*) density at Fire Island, NY, USA in 2016–2022. Survival estimates are from a

modified Dail-Madsen model while other covariates are held at the mean. Solid line depicts mean brood survival. Dark gray ribbon depicts 85% credible intervals and light gray ribbon depicts 95% credible intervals

et al. 2021) and were a negligible component of red fox diet in 2015–2018 (Black 2021). Instead, the increase in cat abundance following the sarcoptic mange epizootics may have resulted from a release of density-dependence. As red foxes declined, cats were no longer excluded from territories previously occupied by red foxes (Molsher 1999; Glen and Dickman 2005), which generally overlapped with areas of high plover nesting density (Walker et al. 2019, 2020; Black 2021).

Our estimation of cat population size is predicated on the assumption that the demographic processes driving the population growth rates from 2015–2018 have not changed. Natural immigration of cats from Long Island is likely rare but not impossible. Feral or free-roaming cats originating from Long Island could cross bridges or sections of the Great South Bay that freeze during winter to reach Fire Island. However, it is more likely that cats are moved to Fire

Island by humans. At the west and east study areas, we observed ear tipping among multiple cats, which is indicative of trap-neuter-release (TNR) operations (Dalrymple et al. 2022). TNR efforts did not stop all cats from breeding, as evidenced by periodic photos of pregnant females and their kittens. If the rate of human-mediated cat ‘immigration’ to Fire Island TNR colonies increased after our trail camera study concluded in 2018, the cat population growth will differ from what we predicted here. Moreover, regular supplemental feeding at TNR colonies could raise cat carrying capacity above the low estimate that we used here. We used 0.079 cats/ha, an estimate of carrying capacity from islands with no to small human populations where cats likely have limited access to anthropogenic subsidies (Flockhart and Coe 2018). Feral and free-roaming cats may have comparatively greater access to feeding and shelters on Fire Island, as the island is a popular vacation destination and

supports multiple residential villages within its interior. Our simple estimation of cat population does not account for density-dependent declines that could be driven by diseases within this system (e.g., sarcoptic mange). While field researchers have not yet observed sickly cats or other evidence of cats nearing carrying capacity, future study is needed to examine cat population dynamics.

Robinson et al. (2024) examined the effect of predator detection rates on plover brood survival using data from this camera trapping study and detected a negative correlation with red fox detection rates, but not cats, from 2015–2018. The negative correlations of cats on plover nest and plover brood survival we find here are explained by an increase in cats in later years (2019–2022) of this study. Red foxes were more abundant than cats in most study areas from 2015–2017 and cats only began to outnumber red foxes in 2018. Although possible in earlier years, we first documented cat depredation of a piping plover in 2018, when field researchers located a scat sample that contained a uniquely-coded plover band that had belonged to a nesting adult (Black 2021). The scat sample containing the plover band was from a cat, as confirmed using molecular methods (Black 2021).

The effects of cats are likely not limited to plover nest and brood survival. We did not attempt to quantify associations of either predator on the survival of adult plovers, and the risk of adult mortality may further vary with the use of nest exclosures (Murphy et al. 2003; Barber et al. 2010; Stantial et al. 2024, cf. Anteau et al. 2022). Depredation of adult plovers can be difficult to detect, though other multi-year studies have confirmed that adult mortality in plovers is correlated with apparent nest abandonment (Neuman et al. 2004; Barber et al. 2010; Roche et al. 2010). At Fire Island, suspected abandonment was the leading cause of nest loss and since the extirpation of red foxes, 18 marked adult plovers from 17 abandoned nests (21.8% of abandoned nests 2019–2023) were not seen again (Wails et al. 2023). Even if cat depredation is rare, indirect effects via landscape of fear, such as dispersal of nesting adults following predator disturbance (e.g., Stantial et al. 2024) and altered behavior of pre-fledged chicks (e.g., Laundré et al. 2010; Robinson et al. 2024), will impact population vital rates.

The plover population at Fire Island has grown considerably following the habitat creation events of

Hurricane Sandy (Robinson et al. 2019, 2020; Walker et al. 2019). Immigration and reproduction drive growth in this population (Robinson et al. 2020). While we report strong, negative correlations of cats on plover reproduction (nest and brood survival), predator activity can further influence avian dispersal and recruitment decisions (Lima 2009). Breeding site fidelity in plovers may decline following poor productivity, nest abandonment, or mate loss (Rioux et al. 2011; Roche et al. 2012; Stantial et al. 2024). Prospective recruits to a breeding population tend to use reproductive and environmental cues to inform future nesting site selection (Pärt et al. 2011; Davis et al. 2017) and the loss of reproductive output may discourage future recruitment into the Fire Island plover population. In general, piping plovers are thought to be habitat limited (Robinson et al. 2019, 2020), but it is possible that very high levels of predation could limit this population. Additional study is needed to develop a more comprehensive understanding of changing plover demography, including changes to adult survival.

Domestic cats are efficient predators that have sizable impacts on native bird populations, depredating an estimated 1.3–4 billion birds annually in the US and extirpating 33 bird species globally from oceanic islands (Loss et al. 2013; Hernandez et al. 2018; Trouwborst et al. 2020). Cats are one of the most damaging invasive predators (Lowe et al. 2000) and the removal of feral and free-roaming individuals substantially benefits native wildlife (Campbell et al. 2011; Jones et al. 2016) and human health (de Wit et al. 2019). Yet, many outdoor cat populations remain unmanaged, even when natural resource managers recognize cats and TNR colonies as an unaddressed threat to conservation (Hunt et al. 2019; Trouwborst et al. 2020; Lepczyk et al. 2022). Here, we have shown cats have a strong, negative association with the nest and brood survival of piping plovers, a species protected under the U.S. Endangered Species Act (USFWS 1985). Further, plovers are present for about four months on the landscape, and Fire Island supports other sensitive wildlife populations (Connor 1971; McElroy et al. 2009). The effects of cats are likely felt in more than just the plover population, as cats are opportunistic generalist predators (Bonnaud et al. 2011; Medina et al. 2011; Lepczyk et al. 2023) that depredate native wildlife even when receiving supplemental feeding at TNR colonies

(Cove et al. 2018; Fieseler 2021). Management action to remove invasive cats from Fire Island – specifically, humanely relocating feral cats, returning free-roaming cats to indoor homes, and preventing future cat population establishment by enforcing state animal abandonment prohibitions and launching community campaigns that promote indoor ownership – is needed to ensure the stability of the plover population and limit the potential effects to other taxa.

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**Data availability** The data that support the findings of this study are available from the corresponding author upon reasonable request.

## Declarations

**Competing interests** The authors have no competing interests to disclose. The findings and conclusions in this article are those of the authors and do not represent the official views of the U.S. Fish and Wildlife Service.

**Ethical approval** All field methods were approved by Virginia Tech's Institutional Animal Care and Use Committee (11-027-FIW, 14-003, 15-119, 16-244, 19-248, 22-190). Fieldwork was conducted under USGS Bird Banding permit #21446, USFWS Endangered Species permits (#TE-697823 and #ESPER0033920), NPS Scientific Research and Collecting permits (FIIS-2013-SCI-002, FIIS-2015-SCI-0011, FIIS-2015-SCI-0020, FIIS-2016-SCI-0003, FIIS-2017-SCI-0004, FIIS-2018-SCI-0004, FIIS-2021-SCI-0003, FIIS-2022-

SCI-0005, FIIS-2023-SCI-0003), New York Department of Environmental Conservation (licenses 126 and 314), New York State Office of Parks, Recreation and Historic Preservation (permit # 15-0700, 16-0379, 16-0393, 17-0637, 17-0753/0755, 18-0168, 19-0128, 21-0131, 22-0040, 23-0058), and with approval from Suffolk County Parks.

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