

See discussions, stats, and author profiles for this publication at: <https://www.researchgate.net/publication/365015476>

Piping plover chick ecology following landscape-level disturbance

Article in *Journal of Wildlife Management* · October 2022

DOI: 10.1002/jwmg.22325

CITATIONS

4

READS

101

8 authors, including:



Samantha Robinson

U.S. Fish and Wildlife Service

28 PUBLICATIONS 429 CITATIONS

[SEE PROFILE](#)



Katie Walker

Virginia Tech

7 PUBLICATIONS 69 CITATIONS

[SEE PROFILE](#)



Henrietta Bellman

Delaware Department of Natural Resources and Environmental Control

10 PUBLICATIONS 77 CITATIONS

[SEE PROFILE](#)



Sarah Karpanty

Virginia Tech

132 PUBLICATIONS 3,550 CITATIONS

[SEE PROFILE](#)

RESEARCH ARTICLE



Piping plover chick ecology following landscape-level disturbance

Samantha G. Robinson | Katie M. Walker | Henrietta A. Bellman |
Daniel Gibson | Daniel H. Catlin | Sarah M. Karpanty |
Shannon J. Ritter | James D. Fraser

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

Correspondence

Samantha G. Robinson, Delaware Division of
Fish and Wildlife, 6180 Hay Point Landing
Road, Smyrna, DE 19977, USA.
Email: samgr@vt.edu

Present address

Samantha G. Robinson and Henrietta A.
Bellman, Division of Fish and Wildlife,
Delaware Department of Natural Resources
and Environmental Control, 6180 Hay Point
Landing Road, Smyrna, DE 19977, USA.

Katie M. Walker, Chincoteague National
Wildlife Refuge, United States Fish and
Wildlife Service, 8231 Beach Road,
Chincoteague, VA 23336, USA.

Funding information

U.S. Fish and Wildlife Service,
Grant/Award Numbers: F15AC00393,
F13AC00194; U.S. Army Corps of Engineers,
Grant/Award Number: W16R0E30650111

Abstract

Population declines of disturbance-dependent species due to suppression of natural disturbances are realized across ecosystems. The piping plover (*Charadrius melodus*; plover), a disturbance-dependent and conservation-reliant shorebird that nests on sandy beaches and barrier islands on the Atlantic Coast, was listed under the United States Endangered Species Act in 1986. In 2012, Hurricane Sandy landed on Fire and Westhampton islands, barrier island nesting sites for plovers in New York, USA. Hurricane Sandy was a natural disturbance in this system, creating abundant nesting habitat. The number of chicks produced by a pair, or a population, is a direct measure of reproductive output, and gaining a better understanding of productivity and chick behavior following large-scale habitat creation may improve plover habitat management and potentially species persistence. We evaluated the effects of landscape features on habitat selection, behavior, and survival of plover broods using logistic regression, generalized linear mixed effects models, and survival models. Plover broods selected flatter sites with less dense vegetation than available at random. Chick foraging rates were highest in moist substrates and were lower in areas of higher nesting plover density. Chick survival was greater for broods that hatched earlier in the breeding season and increased as chicks aged.

This is an open access article under the terms of the Creative Commons Attribution-NonCommercial-NoDerivs License, which permits use and distribution in any medium, provided the original work is properly cited, the use is non-commercial and no modifications or adaptations are made.

© 2022 The Authors. *The Journal of Wildlife Management* published by Wiley Periodicals LLC on behalf of The Wildlife Society.

Generally, providing access to sites with flatter, moist substrates will likely result in higher quality brood rearing habitat on the landscape. Ultimately, vegetation removal and habitat management may be needed to reduce plover nesting density and ensure sufficient habitat, which may in turn improve plover chick survival. Moreover, sustaining natural landscape disturbances such as those resulting from storms, and not taking actions to prevent hurricane-created overwash, will allow these landscape features to persist.

KEYWORDS

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

Changes in landscape characteristics, particularly habitat losses, are among the most influential contributors to wildlife population changes (Bonnot et al. 2017, Bar-Massada et al. 2019). To maximize species persistence probability, a thorough understanding of landscape effects at all life stages is desirable (Norris and Marra 2007). This need is particularly true for conservation-reliant species, as conservation funding is limited and thus must be targeted efficiently (Goble et al. 2012). Most early successional, or disturbance-dependent species live in landscapes that are dynamic in space and time (Hunter et al. 2001), and many are in decline or have become extinct, in part due to human suppression of natural disturbance (Hunter et al. 2001). Barrier islands are highly dynamic, narrow, low-lying strips of sand that occur adjacent to the mainland in some coastal systems and are continuously transformed by storm and wave action (Leatherman 1988). Storm-related annual variations result in geomorphic changes to the landscape (Maslo et al. 2019). Thus, to properly manage a landscape following a disturbance, it is important to understand how species interact with and use disturbed habitat, and how these changes affect all life-stage vital rates and behavior (Miguet et al. 2016).

Piping plovers (*Charadrius melodus*; plover), temperate breeding shorebirds that occur on barrier islands in parts of their range, experienced range-wide population declines prior to their listing under the United States Endangered Species Act in 1986 (U.S. Fish and Wildlife Service [USFWS] 1985). For the Atlantic Coast population, declines were primarily attributed to habitat loss, human disturbance, and predation (USFWS 1996). Despite widespread management and substantial population increases in portions of their range, active management may always be required for this conservation-reliant species (Scott et al. 2010, Goble et al. 2012). To reduce reliance on persistent active management, it will be most effective to determine which management actions would deliver long-term enhancements to population recovery, such as widespread habitat creation or improvement (Goble et al. 2012). For plovers on the Atlantic Coast, hurricanes and other storms naturally create habitat, allowing populations to rapidly increase for years following habitat creation events (Wilcox 1959; Cohen et al. 2009; Robinson et al. 2019, 2020a). One such event, Hurricane Sandy, landed in the northeast United States in October 2012, causing widespread damage to infrastructure and landscape-level changes to ecosystems, which affected the barrier island chains south of Long Island, New York, where plovers nest (Smallegan et al. 2016, Walker et al. 2019, Zeigler et al. 2019). Following this event, the number of nesting plover pairs in the area substantially increased from prior to Hurricane Sandy, in 2012, through at least 2019 (Robinson et al. 2020a). Furthermore, management and monitoring were mandated on the island following the initiation of the Fire Island to Moriches Inlet Stabilization Project, an island-wide project with the goal of stabilizing the island against future storm effects, increasing potential relevancy of studies to plover site managers (USFWS 2014).

The effects of landscape characteristics on plover nest site selection and survival to hatch have been extensively evaluated, but there is comparably limited spatially explicit study of their impacts on other life stages (i.e., adults, chicks; Maslo et al. 2016, Zeigler et al. 2017, Walker et al. 2019). Furthermore, adult survival likely is

driven by flyway-wide conditions, making it challenging to evaluate the effect on survival in local conditions (Norris 2005; Gratto-Trevor et al. 2012; Gibson et al. 2018, 2019; Weithman et al. 2018). Alternatively, variation in chick behavior and survival primarily are driven by local characteristics and therefore are more manageable on the breeding grounds (Haffner et al. 2009, Anteau et al. 2014, Stantial et al. 2021). Further, the chick-rearing period drives reproductive output and influences population growth, and therefore more study is warranted (USFWS 1985). Understanding plover chick response to a newly disturbed landscape through time will allow site managers to focus management strategies towards the most influential landscape features.

Population change in plovers is correlated with reproductive output, which is comprised of nest and chick survival (Saunders et al. 2018, Robinson et al. 2020a). For plovers, nest survival is high where predator exclosures are used (Melvin et al. 1992); however, once chicks hatch and begin to forage for themselves, the nest exclosure no longer protects them (Melvin et al. 1992). Plover chick survival could be influenced by habitat suitability (Catlin et al. 2019) and would be reduced if chicks did not have access to adequate foraging habitat (Elias et al. 2000, Catlin et al. 2014, Walker et al. 2019). Disturbance can cause reduced chick survival in plovers (DeRose-Wilson et al. 2018) and chick survival can vary greatly between breeding sites within a year (Weithman et al. 2019). In addition, chick survival in plovers in the Central Plains population can be negatively density dependent (Hunt et al. 2018), although this relationship may be variable by degrees of density and landform (Anteau et al. 2014). Understanding the effect of landscape features on plover chick survival also can determine whether habitat may be limited or alternatively, if habitat characteristics are acting as an ecological trap (Wiltermuth et al. 2015, Hale and Swearer 2016). Therefore, the next step in understanding variation in chick survival is to understand how habitat is interacting with density, human disturbance, and changing landscape features at fine scales. In addition, understanding habitat selection and foraging behavior of broods in a changing landscape following widespread disturbance could help managers increase survival of plover chicks under varying conditions.

Habitat features likely interact with density, predation, and disturbance and their effects on plover chick habitat selection (Flemming et al. 1988, Anteau et al. 2014, DeRose-Wilson et al. 2018, Walker et al. 2019). Following a large-scale habitat creating event, the landscape will change over time, potentially reducing habitat. Declines in habitat quantity and suitability can result in increased nesting density, lower carrying capacity, and increased intra- and interspecific aggression for density-dependent species (Royama 1977, Cubaynes et al. 2014, Goyert et al. 2017). Declines in habitat also can reduce the effectiveness of camouflage and increase detection by predators, which may interact with density if predators develop an improved search image of local prey (Gendron and Staddon 1983). Increased human disturbance also may isolate and reduce available habitat if it is made unavailable or unsuitable by temporary obstruction (e.g., beach bathing) or by direct effects on habitat (e.g., rutting from beach driving; DeRose-Wilson et al. 2018, Walker et al. 2019, Stantial et al. 2021). Evaluating whether plover chick habitat selection changes through time following a landscape-scale disturbance can advance the understanding of which factors are most important for improving reproductive output.

Plover chick foraging behavior can influence growth, resulting in differences in survival (Catlin et al. 2014). Like survival, plover behavior frequently has been studied, but habitat characteristics have primarily been assessed at a categorical level (e.g., high vs. low disturbance, wet vs. dry). Behavior is related to human disturbance (Burger 1994, DeRose-Wilson et al. 2018), and habitat (Loefering and Fraser 1995, Goldin and Regosin 1998, Elias et al. 2000, Le Fer et al. 2008a, Stantial et al. 2021), with researchers reporting that plovers respond to and avoid areas with frequent human disturbance and spend more time foraging in moist areas with low wave energy where invertebrates are abundant. Like selection and survival, an improved understanding of plover behavior may benefit from finer scale, spatially explicit analyses.

If it is determined that a specific landscape feature can positively influence reproductive output of plovers, future habitat management can attempt to replicate those features. Furthermore, the landscape-level disturbance created by Hurricane Sandy provided an opportunity to understand how plover chicks

interact with the environment across a gradient of habitat characteristics as time since disturbance increased, and plover nesting densities changed. To improve understanding of the effects of fine-scale, spatially explicit landscape features on piping plover chicks, our objectives were to understand plover chick habitat selection as time since disturbance increased and the influence of post-hurricane landscape features on plover chick survival and behavior. We hypothesized that as the newly disturbed landscape matured, plover chicks would adapt to evolving landscape conditions, and that would be apparent in trends in habitat selection, survival, and foraging behavior, likely most noticeably in relationships towards vegetation and dry sand abundance. Plover broods and the adults tending them likely are selecting habitat to maximize survival and foraging opportunities (Orians and Wittenberger 1991, Fraser and Catlin 2019, Robinson et al. 2021). We hypothesized that chick survival would be lower in areas of more dense vegetation, which can be used as concealment for terrestrial predators, and closer to development, which may attract predators and increase human disturbance. Further, we hypothesized that chick survival would be negatively correlated with plover nesting density because of intra- and interspecific competition for space. We hypothesized that plovers would select areas with higher invertebrate abundance for foraging, such as intertidal regions, particularly moist areas with low wave energy, and that such sites would elicit greater foraging rates (Elias et al. 2000, Le Fer et al. 2008b).

STUDY AREA

We studied plovers on 27 km of Fire and Westhampton islands, barrier islands south of Long Island, New York, USA, during April to August 2013–2019 (Figure 1). The study area consisted of Fire Island National Seashore, Otis Pike Fire Island High Dune Wilderness, managed by the National Park Service, Smith Point and Cupsogue Beach County Parks, managed by Suffolk County Parks, and Robert Moses State Park, managed by New York Parks, Recreation, and Historic Preservation. Monitoring at Robert Moses State Park and the Lighthouse Tract of the Fire Island National Seashore did not begin until 2015, following a study area expansion (Figure 1). All sites were used for recreation at varying times the year, including beach recreation, beach driving, fishing, and camping.

These islands have the Atlantic Ocean to the south and several bays to the north (Figure 1). Land cover types in the study area consisted of ocean-front sandy beaches, dunes, overwashes (areas where storm water carried sand landward over the island to the bay), bay-side sandy beaches, ephemeral pools, and breaches originally formed by Hurricane Sandy that were subsequently filled (Walker et al. 2019). The study area also included 3 inlets: Fire Island Inlet, Old Inlet, and Moriches Inlet. Old Inlet was formed by Hurricane Sandy in 2012 and has been left open, and Moriches and Fire Island inlets are dredged and stabilized with jetties to the east and west. Human use was variable among the management areas with pedestrian and off-road vehicle use on various portions of the beach and boat access along the shoreline (DeRose-Wilson et al. 2018).

During the plover brood rearing period (~May–Aug), minimum temperatures ranged from 4.4–25.0°C and maximum temperatures ranged from 10.6–37.2°C (National Oceanic and Atmospheric Administration [NOAA] 2019). Elevation ranged from 0–10.8 m above sea level. The vegetation community was primarily composed of American beachgrass (*Ammophila breviligulata*), common reed (*Phragmites australis*), seaside goldenrod (*Solidago sempervirens*), beach pea (*Lathyrus japonicus*), and wooly beach heather (*Hudsonia tomentosa*; Klopfer et al. 2002).

Plover chick predators in the study area included red fox (*Vulpes vulpes*), domestic cat, North American raccoon (*Procyon lotor*), common raven (*Corvus corax*), American crow (*C. brachyrhynchos*), peregrine falcon (*Falco peregrinus*), merlin (*F. columbarius*), great horned owl (*Bubo virginianus*), great black-backed gull (*Larus marinus*), herring gull (*L. argentatus*), and Atlantic ghost crab (*Ocypode quadrata*). Early in the study there were high densities of red fox in the study area; however, mange outbreaks in 2015 (east of Old Inlet) and 2017 (west of Old Inlet) significantly reduced the local red fox densities throughout the remainder of the study (Figure 1; Black 2021).

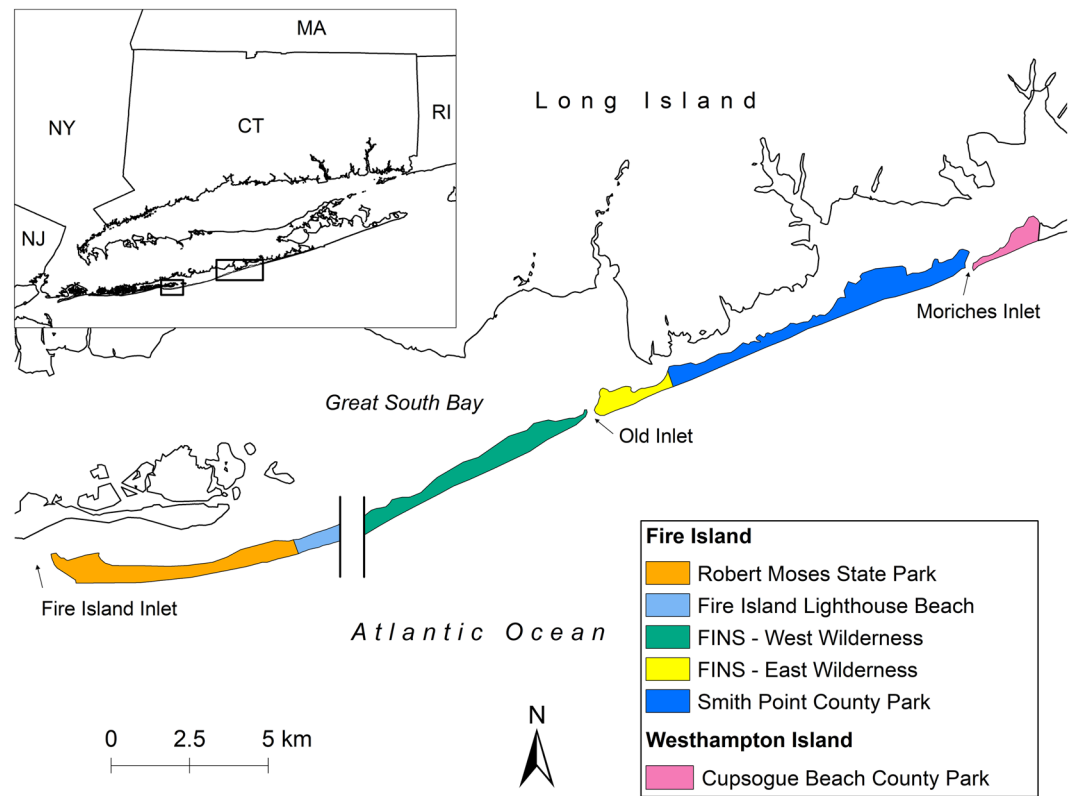


FIGURE 1 Study area on Fire Island and Westhampton Island, New York, USA, where we monitored piping plover broods during 2013–2019 to evaluate survival, habitat selection, and behavior of piping plover broods in response to post-Hurricane Sandy landscape features. We added Robert Moses State Park and the Fire Island Lighthouse Beach to the study in 2015. We delineate the Fire Island National Seashore Otis Pike High Dune Wilderness (FINS) between east and west of Old Inlet because of differences in density calculation and timing of red fox mange outbreaks.

METHODS

Field methods

Plover surveys occurred in designated subsites within the boundaries of management units and were based on local geomorphic qualities (e.g., overwash, restoration area, ocean-front sandy beach). We searched for plover nests using visual observation and by observing adult plover behavior. When we found a nest, we recorded the location using a Garmin (Garmin International, Olathe, KS, USA) or Trimble global positioning system (GPS) unit (Trimble, Sunnyvale, CA, USA). If we found a nest with <4 eggs, we estimated initiation date assuming 1.5 days to lay each egg (Wilcox 1959, Haig and Oring 1988). If we found a nest with 4 eggs, or if after 4 days the clutch did not increase to 4 eggs, we floated eggs to estimate initiation date (Westerkov 1950). We monitored nests every 1–3 days until they hatched or failed and considered nests that hatched ≥ 1 chick to be successful.

We banded all chicks as soon after hatch as possible (age range = 0–14 days) with either a combination of 4-colored Darvic plastic leg bands (2013), or a uniquely identifiable etched Darvic plastic flag with a color band on the opposite leg (2014–2019). We conducted brood surveys every 1–3 days until chicks reached 30 days old by searching for banded chicks and associated adults in plover habitat. Upon observation, we collected brood locations

by collecting an observer's location using a GPS unit and offsetting that location with an azimuth from a compass and a distance estimated using a Nikon 8397 Aculon Laser Rangefinder (Nikon, Minato, Tokyo, Japan; Haffner et al. 2009, Wiltermuth et al. 2015, Robinson et al. 2020b). We considered a plover chick fledged at 25 days after hatch for consistency with past plover studies (Hunt et al. 2013, Catlin et al. 2015).

During each brood survey, we conducted 5-minute behavioral observations of a randomly selected chick in a brood using spotting scopes (DeRose-Wilson et al. 2018). Observations occurred between 0546 and 1720. We recorded foraging behaviors (peck, pull [i.e., pulling worms out of sand], drink) throughout the observation, and every 10 seconds we recorded instantaneous behavior (forage, sit, run, walk, chase, flee, preen, encounter, out of sight), and cover type (dry sand, moist sand, dry vegetation, moist vegetation, wrack [i.e., loose vegetation on the beach]). If a chick was out of sight for ≥ 1 consecutive minute, we concluded the behavioral observations.

Image classification and variable creation

Aerial imagery and Light Detection and Ranging (LiDAR) elevation were collected February to April of each year, 2013–2019 (Axis Geospatial, Easton, MD, USA). Following methods described by Walker et al. (2019) and Robinson et al. (2021), we categorized land cover classifications from the 15-cm imagery for each year into 5 classes: dry sand, wet sand, vegetation, water, and development (e.g., parking lots, jetties, boardwalks). We decreased the resolution of the classification to 1-m² pixels prior to creation of variable layers using the resample tool in ArcGIS 10.6 (Esri, Redlands, CA, USA).

From these classifications, we created several continuous landscape variable layers. We created a binary raster where a cell value of 1 represented all dry sand or vegetation pixels, and 0 represented all other pixels. This raster extended 500 m beyond our study area, such that we could derive vegetation and dry sand proportion variables. Using the Euclidean distance tool in ArcGIS 10.6, we created layers with each pixel representing the distance to the ocean intertidal, bay intertidal, development, and vegetation. We also created 2 least-cost distance layers to the ocean and bay intertidal using the path distance tool, where the value of each pixel represented the distance it would take a walking plover to access bay or intertidal foraging habitat from that pixel, assuming any 1-m cell classified as vegetation or water was a barrier to movement (Walker et al. 2019). Development in our study area represents human disturbance, as human use of the beach is typically clustered around parking lots and jetties for fishing (DeRose-Wilson et al. 2018), and areas of predation risk because potential chick predators (e.g., raccoons) could cluster around sites of human use if attracted by garbage or other human waste. We used annual LiDAR to create an elevation layer. Extreme high elevation areas may increase detectability by aerial predators, such as gulls (Laridae) or falcons (Cooper et al. 2008), and low elevation sites may be more likely to be moist sand with higher invertebrate abundance. Finally, using the slope tool in ArcGIS 10.6, we derived a slope layer from our elevation layer because less steep areas could be selected because of potential higher invertebrate abundance and ease of access.

We estimated nesting pair density at the management unit scale because these units were either separated by inlets or substantial distance (Figures 1 and 2). Using the region group tool in ArcGIS, we calculated the size of each dry sand patch in our study area using an 8-cell neighbor rule (i.e., cells at a diagonal are considered contiguous patches). We then removed all patches of dry sand with < 1 m² of contiguous dry sand, and we summed the pixels of dry sand to represent available plover nesting habitat. We present density as the number of pairs that nested in the management unit each year (pairs/sand ha).

Habitat selection

To determine the best scale to measure habitat variables, we used brood movement data. Using the geosphere package in R, we calculated the straight-line movement of broods between successive daily observations (time

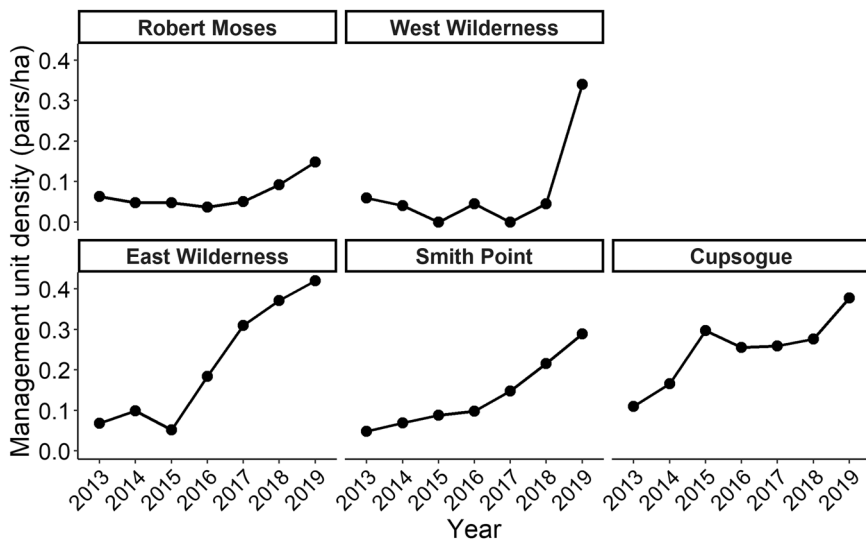


FIGURE 2 Estimated piping plover nesting density by management unit each year following Hurricane Sandy. We studied piping plovers on Fire Island and Westhampton Island, New York, USA, between 2013 and 2019. We defined available habitat as all available dry sand patches $>1 \text{ m}^2$ using 15-cm classified aerial imagery. For 2013 and 2014, the number of pairs was a combination of the number of pairs monitored by Virginia Tech and the number of pairs estimated at Robert Moses State Park and the Lighthouse Tract. We grouped the Lighthouse Tract with Robert Moses State Park for all years. West and East Wilderness are the portions of the Fire Island National Seashore Otis Pike High Dune Wilderness west and east of Old Inlet.

between observations was ~ 1 day) and between observations within a day, during 2014–2019. For daily observations, if we recorded >1 brood location in a day, we selected the last location recorded in a day (Weithman et al. 2020). We divided the distance between locations by the time between observations to scale the observations and removed observations where the time between observations was >24 hours. We also calculated the distance from each brood location to its nest, excluding locations where broods were within 5 m of their nest to account for GPS error (Robinson et al. 2020b). We estimated the mean standardized distance a brood moved in 24 hours, the mean distance a brood moved between locations within a day, and the mean distance a brood was observed from its nest.

We extracted values from each of our variable rasters for the brood and random locations within circular buffers, where the radius was determined by the movement analysis results, using the extract function in the raster package in R (Hijmans 2016). We used 5 m, the average error around GPS locations, as the point scale for distance variables (Robinson et al. 2020b). To evaluate the effect size of each variable, we scaled all continuous variables using the mean and standard deviation.

We used scale optimization to determine the most relevant scale plover chicks selected dry sand and vegetation proportion by developing separate univariate model sets for each (McGarigal et al. 2016). Within a set, each model evaluated plover chick resource selection using 1 of the distances identified in the brood movement analysis as a predictor variable (Chambers et al. 2016, McGarigal et al. 2016). We ranked each model within a set using Deviance Information Criterion (DIC), selecting the best-supported scale (lowest DIC). If there was not one clearly supported scale, we selected the smallest scale with $\leq 5 \Delta \text{DIC}$ because, being a small organism, plovers likely make choices at relatively fine scales (Miguet et al. 2016). To reduce spatial autocorrelation, we spatially rarified the data by removing locations within years, and type of point (brood or random) within 5 m of all other points in the same year and type combination using SDM toolbox for ArcGIS 10.6 (Brown et al. 2017).

We excluded from modeling nest locations and any locations of broods <5 m from their nest within 2 days of hatch to not confound brood habitat selection with nest site selection. We generated 5 times as many random points as used points, restricted to wet or dry sand (Cooper and Millsbaugh 2001). We only assessed resource selection within classified wet and dry sand because land cover-specific plover brood detection probability is unknown but likely lower in vegetated areas. For 2014, we constrained random points to the eastern portion of the study area because plovers were not monitored at Robert Moses State Park until 2015 (Figure 1).

We evaluated habitat selection by comparing plover brood use points to random points distributed in dry and moist sand. We used mixed effect logistic regression models and evaluated 3 models. All models included all continuous landscape variables, 1 model included additive effects of year, 1 included interactive effects with year, and 1 did not include year. We also included a random effect of subsite in all models.

Behavior

To evaluate the effects of landscape characteristics on plover chick behavior, we used 5-minute behavioral observations for broods 3–25 days after hatch and for which we had corresponding location data (Elias et al. 2000). We grouped instantaneous behaviors into 4 groups: foraging, disturbed (encounter, chase, flee, or crouch), undisturbed (run, walk, stand, sit, brood, or preen), and other (Weithman et al. 2020). We grouped broods into categorical cover type (dry sand, dry vegetation, moist sand, moist vegetation, and wrack) based on the cover type that comprised the greatest proportion of time during the behavioral observation. For the total time of the observation, we removed all instances of when the brood was out of sight. Finally, we summarized the proportion of time each behavior was observed in each cover type.

We evaluated chick foraging rates (pecks/min) with linear mixed effects models. We log transformed peck rates (pecks/min). We assessed the effect of the cover type, brood age, quadratic brood age (to account for a non-linear response relative to age), least cost distance to ocean and bay, distance to development and vegetation, slope, elevation, dry sand proportion, and vegetation proportion on foraging rate. We also included weather variables: daily average wind, daily average temperature, and daily precipitation (NOAA 2019). We measured all continuous landscape variables as averages within a circle with a 5-m radius to account for GPS error. We measured the proportion of dry sand and vegetation at the scale selected for habitat selection. We developed an *a priori* model set, with models testing for the effects of year, categorical cover type, continuous cover type, age, quadratic age, all cover type variables, a model that evaluated predator avoidance, a model that evaluated foraging predictors, and a global model with all variables, resulting in 11 models. We included a nested random effect of subsite and brood identification in every model. We scaled all continuous variables using the mean and standard deviation, and we tested for correlation between all continuous variables, removing 1 variable in a pair if correlation between pairs was $|r| \geq 0.6$ (Zuur et al. 2010). We evaluated models based on DIC and considered $\Delta\text{DIC} \leq 5$ competitive.

Survival

We used a modified Dail-Madsen model (Dail and Madsen 2011) informed by repeated counts of the number of chicks observed (y) with a banded parent during the first month of life to estimate pre-fledging chick survival (ϕ) each year from 2013–2019 (Robinson et al. 2020a). In this model, the number of chicks in subsequent period k for brood i in year j ($N_{i,j,k}$) was the sum of the number of chicks that survived and were observed from the previous period ($C_{i,j,k-1}$) and the change in the number of chicks observed between periods ($G_{i,j,k-1}$). The modified model differed from the general Dail-Madsen parameterization because the initial size ($N_{i,j,1}$) of each brood i during each year j was considered a known quantity (i.e., number of hatched eggs) and therefore was not an estimated parameter. Thus, variation in the true number of chicks associated with each brood across time was mediated by

the probabilities of an individual permanently leaving the brood (φ) or joining a brood through brood mixing (π). The number of movements of chicks among broods in this system was previously demonstrated to be approximately 0 (Robinson et al. 2020a); therefore, deviations from the initial brood size were predominantly caused by chick mortality.

$$y_{i,j,k} \sim \text{binomial}(p_{j,k}, N_{i,j,k})$$

$$C_{i,j,k-1} \sim \text{binomial}(\varphi_{j,k}, N_{i,j,k-1})$$

$$G_{i,j,k-1} \sim \text{Poisson}(\pi_{j,k} \times N_{i,j,k-1})$$

$$N_{i,j,k} = C_{i,j,k-1} + G_{i,j,k-1}$$

We estimated daily survival over a 25-day period using 5-day chick detection intervals. To estimate interval-specific chick survival, we developed a model with fixed effects of year and occasion on the survival parameter and a fixed effect of occasion on the detection parameter (p). To estimate the annual probability of survival to fledge (25 days), we calculated the product of the 4 interval survival rates.

We developed 1 model to understand whether chick survival was affected by landscape features, weather, density, or time. We included a linear trend of time, hatch day, maximum temperature, average wind speed, total precipitation, least cost distance to ocean, least cost distance to bay, distance to development, and nesting plover density. We also included a random effect of subsite. We averaged distance and least cost distance variables over the 5-day interval prior to detection and measured them using the methods for habitat selection and behavior.

We built and implemented chick survival, selection, and behavior models in a Bayesian framework, using the jagsUI package to call Jags version 4.3.0 in R 4.0.1 (Kellner 2018, R Core Team 2018). We used vague priors for all estimated parameters. We assessed model fit diagnostics by visually inspecting Markov chain Monte Carlo chains and assuring the convergence ($\hat{R} \leq 1.05$) was reached (Gelman and Rubin 1992). We present estimates using the mean of the posterior distributions and the 95% Bayesian credible intervals.

RESULTS

During 2013–2019, we monitored 234 broods, 11 of which were from 2013 when behavioral observations and locations were not recorded. During 2014–2019, we recorded 2,743 locations and 1,542 behavioral observations of pre-fledged plover chicks.

Habitat selection

The average age of broods during observations was 10.9 days (SD = 7.8), and the mean interval between observations was 1.7 days (SD = 1.4, median = 1.2). From locations where we observed broods on subsequent days ($n = 1,047$), mean daily movement was 132 m (SE = 5) and we observed broods on average 224 m (SE = 7) from their nest. Within a day, the average time between locations was 60 minutes ($n = 378$, SE = 6) and broods moved on average 98 m (SE = 6). Therefore, from movement results, we used average movement distances of 98 m, 132 m, and 224 m as circle radii to evaluate the proper scale to evaluate dry sand and vegetation around brood and random locations. Of these 3 scales, the best scale to evaluate dry sand proportion around brood and random locations was 224 m, and the best scale for vegetation was 98 m (Tables S1–S2, available in Supporting Information). Euclidean distances to ocean and bay were correlated with their respective least cost distance variables, so we retained the least cost distance variables in the model, as plover chicks cannot fly and are therefore more likely to perceive the landscape from a path-perspective.

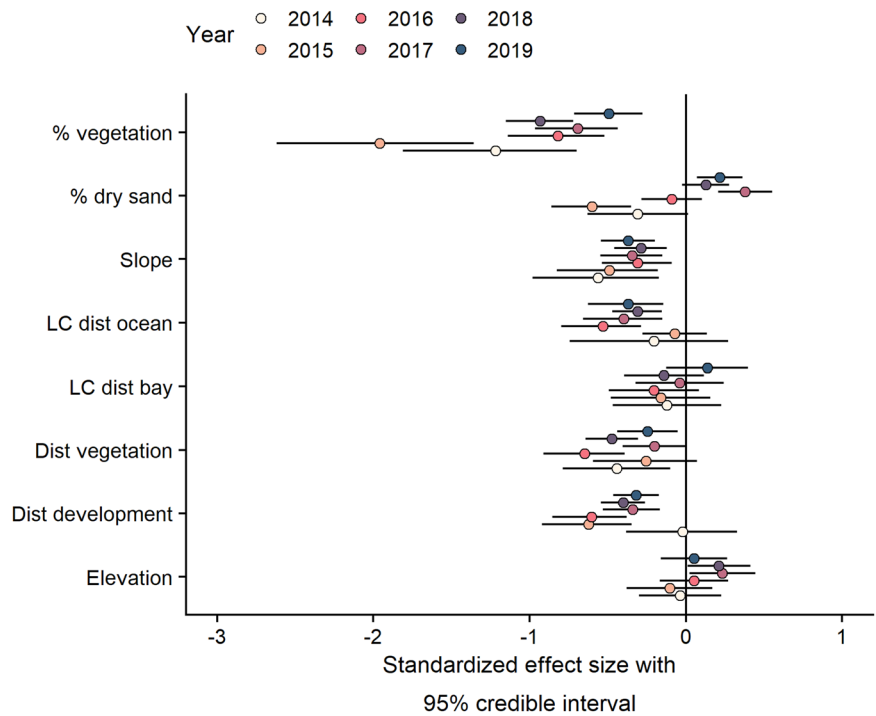


FIGURE 3 Standardized effect size for the top ranked logistic regression habitat selection function describing piping plover brood habitat selection on Fire Island and Westhampton Island, New York, USA, 2013–2019. We abbreviate least cost as LC and distance as dist. For distance variables, a negative effect suggests selection closer to the feature and for proportion variables, a positive effect indicates selection with more of the feature within the specified buffer.

Our best supported model to evaluate resource selection of plover broods included an interaction between all continuous variables and year. The year + predictors model ($\Delta\text{DIC} = 95.81$) and the predictors model ($\Delta\text{DIC} = 162.95$) were not competitive. Avoidance of areas with more vegetation had the greatest effect on chick habitat selection, particularly in 2014 and 2015, such that selection decreased 0.39–0.86% with a 20% increase in vegetation (Figure 3; Table S3, available in Supporting Information). Contrary to vegetation proportion, plover chicks avoided areas farthest from vegetation and selected for flatter sites in all years, with selection decreasing as much as 36% as chicks got as little as 40 m from vegetation (Figure 3, Table S3, available in Supporting Information).

Plover broods avoided areas with more dry sand than other land cover types in 2014–2016, but broods avoided areas with less dry sand beginning in 2017. During 2015–2019, there was a pattern of broods selecting for areas closer to development (Figure 3). Broods in 2014–2018 selected areas closer to the bay intertidal than random, and in 2016–2019 broods were selecting areas closer to the ocean intertidal than random locations. Finally, during 2017 and 2018, broods were selecting higher elevation sites.

Behavior

During 2014–2019, we recorded 1,290 behavioral observations of chicks 3–25 days old, for which we had corresponding location data. Plover chicks spent the most time foraging when in moist sand (23.1%). Chicks spent the most time

disturbed in dry vegetation (1.43%), although overall, chicks spent little time disturbed (1.40% of observations; Table 1). Foraging rates (pecks/min) were greatest in moist vegetation, followed by moist sand, and lowest in dry sand (Table 2).

Variation in peck rates was best described by the global model, which included continuous and categorical cover type variables, year, plover nesting density, weather, and age (Table 3). The cover type that broods spent most of the behavior observation in was more influential to foraging rate than the continuous landscape variables (Figure 4). Peck rates were greater in moist vegetated areas, increasing 25% in moist vegetation as compared to wrack. Peck rates were also greater at lower elevations, with a 1-m decrease in elevation resulting in 8% lower peck rates, and declined as much as 12% with an 11% increase in nesting density (Figure 4; Table S4, available in Supporting Information). Foraging rates also initially increased as plovers aged, but declined as plover chicks reached fledgling age, and were not substantially affected by weather, date, or year.

Survival

Chick survival to fledge was variable among years, with the lowest survival rate in the first year of the study, 2013, and the highest rate in 2018 (Figure 5). Detection probability was high (0.91–0.94) and did not vary

TABLE 1 Proportion of time piping plover broods were observed foraging, undisturbed, and disturbed in each cover type during a 5-minute behavioral observation. We collected data on piping plover broods on Fire Island and Westhampton Island, New York, USA, 2014–2019, as part of a larger study to understand piping plover response to Hurricane Sandy-induced habitat change. Foraging meant a chick was observed pecking, probing, or drinking, undisturbed was run, walk, stand, sit, brood, or preen, and disturbed was encounter, chase, flee, or crouch.

Cover type	Foraging		Undisturbed		Disturbed	
	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
Dry sand	0.11	0.0056	0.76	0.0086	0.014	0.0021
Dry vegetation	0.10	0.0096	0.68	0.0190	0.014	0.0054
Moist sand	0.23	0.0110	0.67	0.0130	0.014	0.0037
Moist vegetation	0.19	0.0460	0.56	0.0610	0.008	0.0057
Wrack	0.15	0.0067	0.75	0.0095	0.013	0.0024
All cover types	0.14	0.0041	0.73	0.0057	0.014	0.0014

TABLE 2 Mean foraging attempts (peck, probe, pull) per minute (pecks/min) for the dominant cover type during piping plover brood observations. We collected data on piping plover broods on Fire Island and Westhampton Island, New York, USA, 2014–2019, as part of a larger study to understand piping plover response to Hurricane Sandy-induced habitat change.

Majority cover type	n	Foraging rate (pecks/min)		
		$\bar{x}$	SE	Max.
Dry sand	537	4.90	0.23	36.00
Dry vegetation	155	5.29	0.44	26.40
Moist sand	259	10.90	0.47	48.20
Moist vegetation	16	12.40	1.75	28.20
Wrack	323	6.70	0.26	22.40

TABLE 3 Model selection table for models describing cover type, weather, age, density, and year effects on piping plover brood foraging rates (pecks/min) on Fire and Westhampton islands, New York, USA, 2014–2019. Continuous cover type included least cost distance to bay intertidal, least cost distance to ocean intertidal, distance to vegetation, distance to development, slope, elevation, percent sand, percent vegetation, and nesting plover density. Categorical cover type was defined by the cover type most of the behavioral observation occurred in (dry sand, dry vegetation, moist sand, moist vegetation, wrack). Global model included all continuous cover type, categorical cover type, age, year, density, and weather covariates.

Model	K^a	ΔDIC^b
Global	27	0.00
Global–year	21	10.93
Categorical cover type	7	34.69
Cover type (continuous + categorical)	16	37.07
Age + age ²	5	188.25
Foraging (least cost distance + elevation + slope)	7	216.15
Year	8	227.23
Weather	6	233.07
Age	4	233.80
Continuous cover type	12	237.02
Predators (% sand + % vegetation + density)	6	249.48

^aNumber of parameters.

^bDifference in Deviance Information Criterion.

substantially by occasion. Broods that hatched earlier in the summer had a higher probability of surviving to fledge than chicks hatching later (hatching 2 weeks later resulted in a 31% lower probability of survival), and the probability of a brood surviving to fledge increased as much as 70% once chicks were 6 days old (Table S5, available in Supporting Information). Chick survival also increased with increasing temperatures and at flatter sites (Figure 6). Chicks farther from the bay and in areas of lower elevation during a 5-day detection window had higher survival.

DISCUSSION

Habitat selection

The proportion of an area covered by vegetation was highly influential to plover chick habitat selection. Plover use decreased as the proportion of vegetation increased, indicating avoidance of densely vegetated areas. Despite this, in most years, plover chicks selected for sites closer to vegetation patches, measured as 1-m² patches, than expected at random. These findings indicate that the relationships between plover chicks and vegetation are complex. For plover chicks, dense vegetation likely represents an area of high predation risk as vegetation can conceal terrestrial predators (Camp et al. 2012, Wiltermuth et al. 2015). As such, plover chicks are likely selecting sites with high visibility to detect predators but may prefer some vegetation patches closer for concealment when needed. As time since Hurricane Sandy increased, avoidance of densely vegetated areas declined. When less-dense vegetation patches are available, such as immediately following the Hurricane, broods may select for these areas but can exhibit plasticity as the vegetation density on the landscape increases

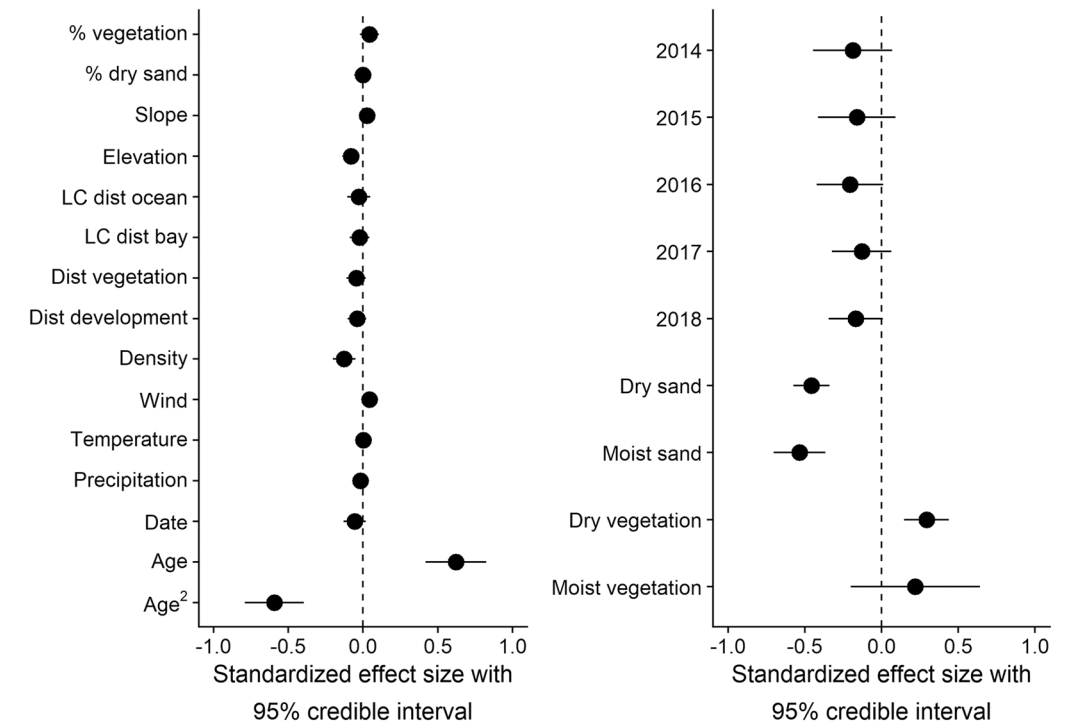


FIGURE 4 Standardized beta coefficients describing the relationships between piping plover chick peck rates (pecks/min) and categorical (right) and continuous (left) variables. We abbreviate least cost as LC and distance as dist. We studied piping plovers on Fire Island and Westhampton Island, New York, USA, 2013–2019, following landscape change due to Hurricane Sandy. Model estimates are from a linear mixed effects model. Dry sand was the reference cover type category, and 2019 was the reference year category. Significance is interpreted as no overlap between 95% credible intervals and 0, represented by the dashed vertical line.

(Elias et al. 2000, Morelli 2012). The decrease in avoidance of larger vegetation patches also corresponded with a decrease in the red fox population on Fire Island (Black 2021), and therefore may indicate a movement towards avoidance of aerial predators such as falcons, as vegetation would reduce detection of chicks from above. Chicks also selected areas of more dry sand, relative to all other cover types combined, later in the study, indicating it is important for chicks to remain inconspicuous and be able to detect predators (Camp et al. 2012, Claassen et al. 2018, Fraser and Catlin 2019). Smaller patches of vegetation also likely serve as a source of food for plover chicks, as they can glean invertebrates off plants (Cuthbert et al. 1999). Selection for flatter areas suggests preference for sites of moist substrate and avoidance of dry dunes. The relationship between plover broods and flatter sites with less vegetation is seen across plover breeding populations (Wiltermuth et al. 2015). Moist substrates in plover habitats tend to have higher invertebrate abundances (Loefering and Fraser 1995, Elias et al. 2000, Cohen et al. 2009, DeRose-Wilson et al. 2018), and thus broods likely are cuing in on this essential resource for growth (Catlin et al. 2014).

Behavior

Plover chick foraging rates were best explained by the dominant cover type during behavioral observations. Foraging rates were greatest in moist vegetation, including wrack, which is similar to findings of other plover

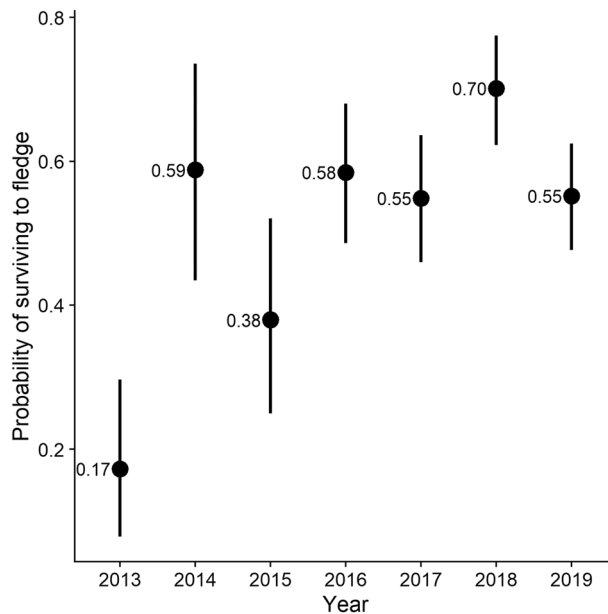


FIGURE 5 Probability of surviving to fledge (25 days) for piping plover chicks, 2013–2019, on Fire Island and Westhampton Island, New York, USA. Estimates are derived from a Dail-Madsen model modified for chick survival and are the product of the 5-day interval-specific probabilities of survival. Error bars represent 95% credible intervals.

behavior studies (Loefering and Fraser 1995, Goldin and Regosin 1998, Elias et al. 2000). Moist substrates have higher invertebrate densities and thus allow plover chicks to maximize their foraging efficiency, improve their growth rates, and enhancing their chance of survival (Cohen et al. 2009, Catlin et al. 2014, DeRose-Wilson et al. 2018). Peck rates initially increased as plovers aged but eventually decreased as plovers neared fledging. Plover chick growth may be non-linear owing to a series of concurrent mechanisms (e.g., correlation between energy efficiency or heat retention and body size). Thus, as growth curves of older chicks level off because of these competing mechanisms, the resource demands necessary to maintain energy surpluses required for additional growth may also decline, allowing them to spend more time focused on maintenance or watching for predators rather than foraging (Schekkerman and Visser 2001, West et al. 2001, Ricklefs 2003). Alternatively, this convex relationship between foraging rates and age may be due to increased foraging efficiency as plovers age. Larger chicks may be able to access larger prey, reducing the need for frequent foraging attempts, or may have increased prey selectiveness, which has been observed in other shorebirds, such as black-tailed godwit (*Limosa limosa*; Schekkerman and Boele 2009).

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

Generally, broods in this study were disturbed at low levels during behavioral observations and disturbance did not vary by dominant cover type. At Cape Hatteras National Seashore, potential disturbance during behavioral observations were infrequent and did not affect movement rates (Weithman et al. 2020). In Rhode Island, USA,

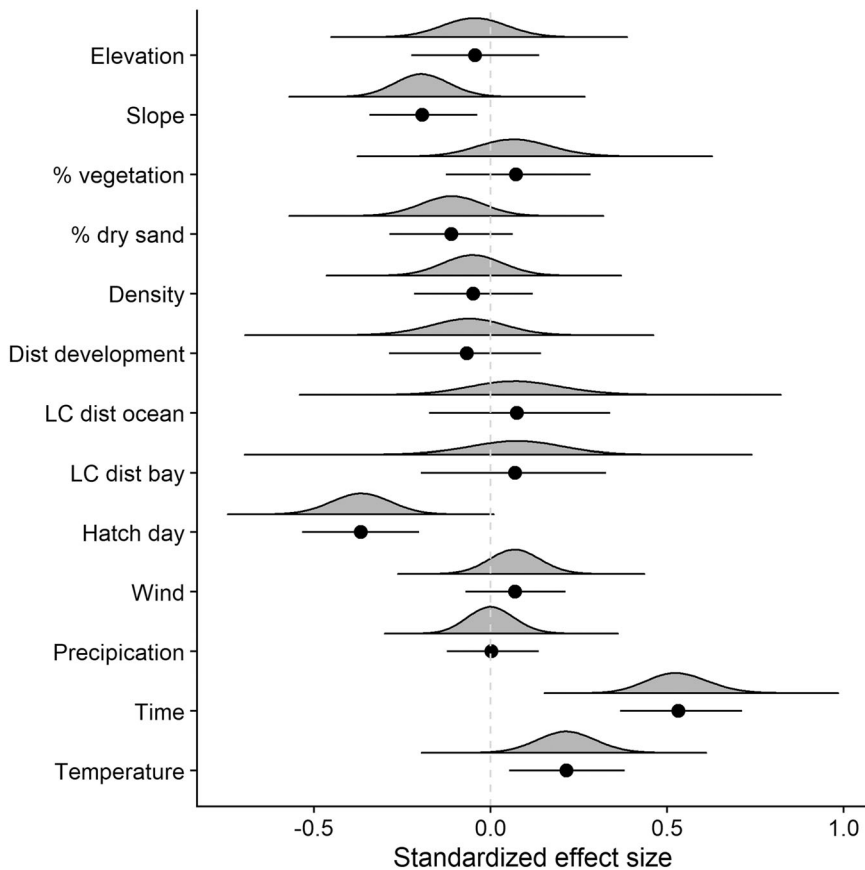


FIGURE 6 Distributions of standardized model coefficients, along with the mean and 95% credible intervals (point and error bars), from a piping plover chick survival model. We studied piping plover broods on Fire Island and Westhampton Island, New York, USA, 2013–2019, to evaluate the response to landscape change following Hurricane Sandy. Model estimates are from a modified Dail-Madsen model. We abbreviate least cost as LC and distance as dist. The time variable was a linear variable testing whether survival increased or decreased as chicks aged, whereas hatch day indicated the effect of the date of hatch on chick survival.

however, broods in mudflats spent less time disturbed (Goldin and Regosin 1998). In New Jersey, USA, moist foraging habitats were the least disturbed (Stantial et al. 2021), and adult plover vigilance was related to the number of people on the beach, regardless of cover type (Burger 1994). In our same study area, foraging rate and the proportion of time spent in moist substrates were lower on days with typically higher disturbance (DeRose-Wilson et al. 2018). The amount of disturbance that plovers experience is site dependent because of site-specific access for people and protection by management. Concurrent analysis of the effects of habitat and disturbance on plover vital rates may further elucidate the ultimate drivers of plover chick behavior on Fire and Westhampton islands.

Survival

Few continuous landscape variables, as measured in this study, were influential to plover chick survival. We observed higher survival when chicks spent more time at flatter and lower elevation sites, which likely corresponds to plover chicks with access to moist substrates having improved foraging prospects. Although relationships with distance to ocean and bay did not appear influential to plover chick survival, others reported that chicks with bayside, as compared to oceanside,

access to habitat have higher survival (Stantial et al. 2021). Rather than the distance to a resource, likely the more important factor for survival is whether a brood is spending time in moist areas with low wave energy. Further evaluating such relationships remains important moving forward to fully understand important landscape drivers of chick survival.

Comparison among analyses

Researchers are making progress on identifying the link between habitat selection and demographic processes (Aldridge and Boyce 2007, Casazza et al. 2011, Catlin et al. 2019). We observed stronger relationships between landscape variables and habitat selection than we did survival, which may indicate that broods are adequately selecting habitat to maximize survival. Alternatively, there are likely many aspects of plover chick ecology that contribute to demography, thus relationships from other aspects than habitat selection could have led to attenuated relationships in demography. Following storm surge from Hurricane Sandy, there was an abundance of habitat (Walker et al. 2019), and following 2015 and 2017, on the east and west sides of Old Inlet respectively, plover broods no longer contended with red fox predation. The influence of increased habitat and primary predator loss was coincident with high chick survival rates, and plasticity in selection for vegetation. The predation pressure in this system is dynamic; therefore, continued study to determine whether increased predation by other predators through mesopredator release (Prugh et al. 2009), or through increased predation pressure by aerial predators, is needed (Whitfield 2003).

That being closer to the bay, as measured by least cost distance, did not positively influence any potential chick metrics, and instead was negatively related to chick survival, suggests that there is habitat located elsewhere in the study area. Plovers elsewhere in the range can flourish despite not having access to bayside habitat (Boettcher et al. 2007, Robinson et al. 2019). In this study, natural overwash and restored habitats were not all characterized by bayside habitat, yet these sites frequently had high reproductive output and high adult fidelity (Robinson et al. 2020a). Further, natural overwash and restoration sites had low human use (DeRose-Wilson et al. 2018), which suggests that human disturbance was more influential than habitat in some cases. In this study, the sites with bayside access were small compared to the rest of the study area, and thus territoriality limited the access of these sites for most pairs. When plover nesting densities were low early in the study, least cost distance to bay was influential in predicting nest site locations (Walker et al. 2019). Prior to Hurricane Sandy, birds did not have access to the bay, and thus made other decisions to optimize their fitness, and persisted, albeit in lower numbers. Therefore, there may be an interaction between nesting density and distance to bayside foraging habitat, the value of being close to bayside habitat is more of a binary variable than a continuous one (i.e., at bayside or not), or the relationships between plover chicks and bayside access is more complex than we represented here.

Overall, of the variables we looked at, the factors primarily driving chick ecology were vegetation and indicators of moist substrates (i.e., slope and elevation). Other researchers have reported that human disturbance also influences chicks in this and other populations (DeRose-Wilson et al. 2018, Stantial et al. 2021). Direct disturbance by humans and predators likely influences all the factors assessed here (DeRose-Wilson et al. 2018). That earlier hatching broods had a greater probability of survival supports the idea that if human disturbance is reduced during the nesting period (i.e., beach driving restrictions), perhaps plover adults may nest earlier and thus give broods a higher chance of survival by successfully reaching older age earlier (Walker et al. 2019). Many other factors could influence greater chick survival earlier in the season such as prey abundance and predator movement, which should be studied in further detail (Stantial et al. 2020, Wilde et al. 2022).

CONSERVATION IMPLICATIONS

Landscape change from Hurricane Sandy resulted in large areas of open dry sand, with some areas allowing large areas of access to low-energy bay foraging habitat and initially low plover nesting densities. The newly disturbed landscape allowed an increase in plover nesting pairs and high chick survival. To improve body condition and

survival of plover chicks through improved foraging rates, maintaining direct access to relatively flat, moist substrates with low vegetation density around them is crucial. In the absence of storms, vegetation removal is needed to maintain access to flat, low elevation, moist substrates and early successional vegetation communities that are preferred by plovers. Removal of dense vegetation also will reduce overall concealment ability of mammalian predators in plover nesting areas.

ACKNOWLEDGMENTS

We thank S. T. Papa, R. J. Smith, and P. M. Weppeler for supporting this work. We thank A. F. McIntyre, T. Byrne, L. Ries, M. S. Bilecki, N. Gibbons, D. Lynch, K. Jennings, and F. C. Hamilton for permission to work on their property and various kinds of support. We thank S. P. Prisley and 2 anonymous reviews for reviewing and improving earlier versions of this manuscript. We thank D. R. Fraser and K. L. Hunt for logistical support during this study, and C. E. Weithman for providing code to summarize our behavioral data. Finally, we thank all the Fire Island technicians and crew leaders that tirelessly collected the field data used in this study. This project was supported by funds provided by the United States Army Corps of Engineers to the USFWS under the Fire Island to Moriches Inlet Biological Opinion, and by Virginia Tech.

CONFLICTS OF INTEREST

The authors declare no conflicts of interest.

ETHICS STATEMENT

All capture, handling, and observation procedures were conducted under Virginia Tech Institutional Animal Care and Use Committee protocols (14-003 and 16-244), a United States Geological Survey Federal Bird Banding permit (21446), a USFWS Endangered Species permit (TE-697823), United States National Park Service Scientific Research and Collecting permits (FIIS-2013-SCI-002, FIIS-2015-SCI-0011, FIIS-2016-SCI-0003, FIIS-2017-SCI-0004, FIIS-2018-SCI-0004), a New York State Department of Environmental Conservation Endangered Species permit (314), New York State Office of Parks, Recreation and Historic Preservation permits (15-0700, 16-0393, 17-0755, 18-0168, 19-0128), and permits for research in Suffolk County Parklands.

DATA AVAILABILITY STATEMENT

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

REFERENCES

- Aldridge, C. L., and M. S. Boyce. 2007. Linking occurrence and fitness to persistence: habitat-based approach for endangered greater sage-grouse. *Ecological Applications* 17:508–526.
- Anteau, M. J., M. T. Wiltermuth, M. H. Sherfy, T. L. Shaffer, and A. T. Pearse. 2014. The role of landscape features and density dependence in growth and fledging rates of piping plovers in North Dakota, USA. *Condor* 116:195–204.
- Bar-Massada, A., A. R. Ives, and V. Butsic. 2019. A mathematical partitioning of the effects of habitat loss and habitat degradation on species abundance. *Landscape Ecology* 34:9–15.
- Black, K. M. 2021. Red fox ecology and interactions with piping plovers on Fire Island, New York. Dissertation, Virginia Tech, Blacksburg, USA.
- Boettcher, R., T. Penn, R. R. Cross, K. T. Terwilliger, and R. A. Beck. 2007. An overview of the status and distribution of piping plovers in Virginia. *Waterbirds* 30:138–151.
- Bonnot, T. W., F. R. Thompson, III, and J. J. Millspaugh. 2017. Dynamic-landscape metapopulation models predict complex response of wildlife populations to climate and landscape change. *Ecosphere* 8:e01890.
- Brown, J. L., J. R. Bennett, and C. M. French. 2017. SDMtoolbox 2.0: the next generation Python-based GIS toolkit for landscape genetic, biogeographic and species distribution model analyses. *PeerJ* 5:e4095.
- Burger, J. 1994. The effect of human disturbance on foraging behavior and habitat use in piping plover (*Charadrius melodus*). *Estuaries* 17:695–701.

- Camp, M. J., J. L. Rachlow, B. A. Woods, T. R. Johnson, and L. A. Shipley. 2012. When to run and when to hide: the influence of concealment, visibility, and proximity to refugia on perceptions of risk. *Ethology* 118:1010–1017.
- Casazza, M. L., P. S. Coates, and C. T. Overton. 2011. Linking habitat selection to brood success in greater sage-grouse. Pages 151–167 in M. K. Sandercock, K. Martin, and G. Segelbacher, editors. *Ecology, conservation, and management of grouse*. University of California Press, Berkeley, USA.
- Catlin, D. H., J. D. Fraser, and J. H. Felio. 2015. Demographic responses of piping plovers to habitat creation on the Missouri river. *Wildlife Monographs* 192:1–42.
- Catlin, D. H., J. D. Fraser, J. H. Felio, and J. B. Cohen. 2011. Piping plover habitat selection and nest success on natural, managed, and engineered sandbars. *Journal of Wildlife Management* 75:305–310.
- Catlin, D., D. Gibson, M. J. Friedrich, K. L. Hunt, S. M. Karpanty, and J. D. Fraser. 2019. Habitat selection and potential fitness consequences of two early-successional species with differing life-history strategies. *Ecology and Evolution* 9: 13966–13978.
- Catlin, D. H., O. Milenkaya, K. L. Hunt, M. J. Friedrich, and J. D. Fraser. 2014. Can river management improve the piping plover's long-term survival on the Missouri River? *Biological Conservation* 180:196–205.
- Chambers, C. L., S. A. Cushman, A. Medina-Fitoria, J. Martínez-Fonseca, and M. Chávez-Velásquez. 2016. Influences of scale on bat habitat relationships in a forested landscape in Nicaragua. *Landscape Ecology* 31:1299–1318.
- Claassen, A. H., J. D. Forester, T. W. Arnold, and F. J. Cuthbert. 2018. Consequences of multi-scale habitat selection on reproductive success of riverine sandbar-nesting birds in Cambodia. *Avian Biology Research* 11:108–122.
- Cohen, J. B., L. M. Houghton, and J. D. Fraser. 2009. Nesting density and reproductive success of piping plovers in response to storm- and human-created habitat changes. *Wildlife Monographs* 173:1–24.
- Cooper, A. B., and J. J. Millspaugh. 2001. Accounting for variation in resource availability and animal behavior in resource selection studies. Pages 243–273 in J. J. Millspaugh and J. M. Marzluff, editors. *Radio tracking and animal populations*. Academic Press, San Diego, California, USA.
- Cooper, W. E., Jr., J. P. Caldwell, and L. J. Vitt. 2008. Escape responses of cryptic frogs (Anura: Brachycephalidae: Craugastor) to simulated terrestrial and aerial predators. *Behaviour* 145:25–38.
- Cubaynes, S., D. R. MacNulty, D. R. Stahler, K. A. Quimby, D. W. Smith, and T. Coulson. 2014. Density-dependent intraspecific aggression regulates survival in northern Yellowstone wolves (*Canis lupus*). *Journal of Animal Ecology* 83: 1344–1356.
- Cuthbert, F. J., B. Scholtens, L. C. Wemmer, and R. McLain. 1999. Gizzard contents of piping plover chicks in northern Michigan. *Wilson Bulletin* 111:121–123.
- Dail, D., and L. Madsen. 2011. Models for estimating abundance from repeated counts of an open metapopulation. *Biometrics* 67:577–587.
- DeRose-Wilson, A. L., K. L. Hunt, J. D. Monk, D. H. Catlin, S. M. Karpanty, and J. D. Fraser. 2018. Piping plover chick survival negatively correlated with beach recreation. *Journal of Wildlife Management* 82:1608–1616.
- Elias, S. P., J. D. Fraser, and P. A. Buckley. 2000. Piping plover brood foraging ecology on New York barrier islands. *Journal of Wildlife Management* 64:346–354.
- Le Fer, D., J. D. Fraser, and C. D. Kruse. 2008a. Piping plover foraging-site selection on the Missouri River. *Waterbirds* 31: 587–592.
- Le Fer, D., J. D. Fraser, and C. D. Kruse. 2008b. Piping plover chick foraging, growth, and survival in the Great Plains. *Journal of Wildlife Management* 72:682–687.
- Flemming, S. P., R. D. Chiasson, P. C. Smith, P. J. Austin-Smith, and R. P. Bancroft. 1988. Piping plover status in Nova Scotia related to its reproductive and behavioral responses to human disturbance. *Journal of Field Ornithology* 59:321–330.
- Fraser, J. D., and D. H. Catlin. 2019. Habitat ecology and conservation of *Charadrius* plovers. Pages 212–244 in M. A. Colwell and S. M. Haig, editors. *The population ecology and conservation of Charadrius plovers*. CRC Press, New York, New York, USA.
- Gelman, A., and D. B. Rubin. 1992. Inference from iterative simulation using multiple sequences. *Statistical Science* 7:457–511.
- Gendron, R. P., and J. E. R. Staddon. 1983. Searching for cryptic prey: the effect of search rate. *American Naturalist* 121: 172–186.
- Gibson, D., M. K. Chaplin, K. L. Hunt, M. J. Friedrich, C. E. Weithman, L. M. Addison, V. Cavalieri, S. Coleman, F. J. Cuthbert, J. D. Fraser, et al. 2018. Impacts of anthropogenic disturbance on body condition, survival, and site fidelity of nonbreeding piping plovers. *Condor: Ornithological Applications* 120:566–580.
- Gibson, D., A. D. Hornsby, M. B. Brown, J. B. Cohen, L. R. Dinan, J. D. Fraser, M. J. Friedrich, C. L. Gratto-Trevor, K. L. Hunt, M. Jeffery, et al. 2019. Migratory shorebird adheres to Bergmann's rule by responding to environmental conditions through the annual lifecycle. *Ecography* 42:1482–1493.
- Goble, D. D., J. A. Wiens, J. M. Scott, T. D. Male, and J. A. Hall. 2012. Conservation-reliant species. *BioScience* 62:869–873.
- Goldin, M. R., and J. V. Regosin. 1998. Chick behavior, habitat use, and reproductive success of piping plovers at Goosewing Beach, Rhode Island. *Journal of Field Ornithology* 69:228–234.

- Goyert, H. F., E. O. Garton, B. A. Drummond, and H. M. Renner. 2017. Density dependence and changes in the carrying capacity of Alaskan seabird populations. *Biological Conservation* 209:178–187.
- Gratto-Trevor, C. L., D. L. Amirault-Langlais, D. H. Catlin, F. J. Cuthbert, J. D. Fraser, S. B. Maddock, E. A. Roche, and F. Shaffer. 2012. Connectivity in piping plovers: do breeding populations have distinct winter distributions? *Journal of Wildlife Management* 76:348–355.
- Haffner, C. D., F. J. Cuthbert, and T. W. Arnold. 2009. Space use by Great Lakes piping plovers during the breeding season. *Journal of Field Ornithology* 80:270–279.
- Haig, S. M., and L. W. Oring. 1988. Mate, site, and territory fidelity in piping plovers. *Auk* 105:268–277.
- Hale, R., and S. E. Swearer. 2016. Ecological traps: current evidence and future directions. *Proceedings of the Royal Society B: Biological Sciences* 283:20152647.
- Hijmans, R. J. 2016. Raster: geographic data analysis and modeling. R package version 2.5-8. <https://CRAN.R-project.org/package=raster>
- Hogan, B. R., M. M. Grigione, M. A. Marconi, R. E. Thomas, and R. J. Sarno. 2018. Asymmetric antagonism between piping plovers (*Charadrius melodus*) and American oystercatchers (*Haematopus palliatus*), New York, USA. *Waterbirds* 41: 443–448.
- Hunt, K. L., D. H. Catlin, J. H. Felio, and J. D. Fraser. 2013. Effect of capture frequency on the survival of piping plover chicks. *Journal of Field Ornithology* 84:299–303.
- Hunt, K. L., J. D. Fraser, M. J. Friedrich, S. M. Karpanty, and D. H. Catlin. 2018. Demographic response of piping plovers suggests that engineered habitat restoration is no match for natural riverine processes. *Condor* 120:149–165.
- Hunter, W. C., D. A. Buehler, R. A. Canterbury, J. L. Confer, and P. B. Hamel. 2001. Conservation of disturbance-dependent birds in eastern North America. *Wildlife Society Bulletin* 29:440–445.
- Kellner, K. 2018. jagsUI: a wrapper around 'rjags' to streamline 'JAGS' analyses (version 1.5.0). <https://CRAN.R-project.org/package=jagsUI/>
- Klopfer, S. D., A. Olivero, L. Sneddon, and J. Lundgren. 2002. Final Report of the NPS Vegetation Mapping Project at Fire Island National Seashore. Virginia Polytechnic Institute and State University. Blacksburg, USA.
- Leatherman, S. P. 1988. Barrier island handbook. University of Maryland, College Park, USA.
- Loefering, J. P., and J. D. Fraser. 1995. Factors affecting piping plover chick survival in different brood-rearing habitats. *Journal of Wildlife Management* 59:646–655.
- Maslo, B., K. Leu, C. Faillace, M. A. Weston, T. Pover, and T. A. Schlacher. 2016. Selecting umbrella species for conservation: a test of habitat models and niche overlap for beach-nesting birds. *Biological Conservation* 203:233–242.
- Maslo, B., K. Leu, T. Pover, M. A. Weston, B. L. Gilby, and T. A. Schlacher. 2019. Optimizing conservation benefits for threatened beach fauna following severe natural disturbances. *Science of the Total Environment* 649:661–671.
- McGarigal, K., H. Y. Wan, K. A. Zeller, B. C. Timm, and S. A. Cushman. 2016. Multi-scale habitat selection modeling: a review and outlook. *Landscape Ecology* 31:1161–1175.
- Melvin, S. M., L. H. MacIvor, and C. R. Griffin. 1992. Predator exclosures: a technique to reduce predation at piping plover nests. *Wildlife Society Bulletin* 20:143–148.
- Miguet, P., H. B. Jackson, N. D. Jackson, A. E. Martin, and L. Fahrig. 2016. What determines the spatial extent of landscape effects on species? *Landscape Ecology* 31:1177–1194.
- Morelli, F. 2012. Plasticity of habitat selection by red-backed shrikes (*Lanius collurio*) breeding in different landscapes. *Wilson Journal of Ornithology* 124:51–56.
- National Oceanic and Atmospheric Administration [NOAA]. 2019. National Centers for Environmental Information. Daily temperature and precipitation for Westhampton, New York. <https://www.ncdc.noaa.gov/cdo-web/>. Accessed 4 Jun 2019.
- Norris, D. R. 2005. Carry-over effects and habitat quality in migratory populations. *Oikos* 109:178–186.
- Norris, R. D., and P. P. Marra. 2007. Seasonal interactions, habitat quality, and population dynamics in migratory birds. *Condor* 109:535–547.
- Orians, G. H., and J. F. Wittenberger. 1991. Spatial and temporal scales in habitat selection. *American Naturalist* 137: S29–S49.
- Prugh, L. R., C. J. Stoner, C. W. Epps, W. T. Bean, W. J. Ripple, A. S. Laliberte, and J. S. Brashares. 2009. The rise of the mesopredator. *BioScience* 59:779–791.
- R Core Team. 2018. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria
- Ricklefs, R. E. 2003. Is rate of ontogenetic growth constrained by resource supply or tissue growth potential? A comment on West et al.'s model. *Functional Ecology* 17:384–393.
- Robinson, S., H. Bellman, K. Walker, D. Catlin, S. Karpanty, S. Ritter, and J. Fraser. 2021. Adult piping plover habitat selection varies by behavior. *Ecosphere* 12:e03870.

- Robinson, S., J. Fraser, D. Catlin, S. Karpanty, J. Altman, R. Boettcher, K. Holcomb, C. Huber, K. Hunt, and A. Wilke. 2019. Irruptions: evidence for breeding season habitat limitation in piping plovers. *Avian Conservation and Ecology* 14:19.
- Robinson, S. G., D. Gibson, T. V. Riecke, J. D. Fraser, H. A. Bellman, A. DeRose-Wilson, S. M. Karpanty, K. M. Walker, and D. H. Catlin. 2020a. Piping plover population change in a hurricane-affected population and the relation to constructed nesting habitat. *Condor: Ornithological Applications* 122:4.
- Robinson, S. G., C. E. Weithman, H. A. Bellman, S. P. Prisle, J. D. Fraser, D. H. Catlin, and S. M. Karpanty. 2020b. Assessing error in locations of conspicuous wildlife using handheld GPS units and location offset methods. *Wildlife Society Bulletin* 44:163–172.
- Royama, T. 1977. Population persistence and density dependence. *Ecological Monographs* 47:1–35.
- Saunders, S. P., F. J. Cuthbert, and E. F. Zipkin. 2018. Evaluating population viability and efficacy of conservation management using integrated population models. *Journal of Applied Ecology* 55:1380–1392.
- Schekkerman, H., and A. Boele. 2009. Chicks of the black-tailed godwit *Limosa limosa*: vulnerability to weather and prey size. *Journal of Avian Biology* 40:369–379.
- Schekkerman, H., and G. H. Visser. 2001. Prefledging energy requirements in shorebirds: energetic implications of self-feeding precocial development. *Auk* 118:944–957.
- Scott, J. M., D. D. Goble, A. M. Haines, J. A. Wiens, and M. C. Neel. 2010. Conservation-reliant species and the future of conservation. *Conservation Letters* 3:91–97.
- Smallegan, S. M., J. L. Irish, A. R. Van Dongeren, and J. P. Den Bieman. 2016. Morphological response of a sandy barrier island with a buried seawall during Hurricane Sandy. *Coastal Engineering* 110:102–110.
- Stantial, M. L., J. B. Cohen, A. J. Darrah, S. Farrell, and B. Maslo. 2020. Red fox use of landscapes with nesting shorebirds. *Journal of Wildlife Management* 84:1536–1547.
- Stantial, M. L., J. B. Cohen, A. J. Darrah, S. Farrell, and B. Maslo. 2021. Habitat-specific behavior, growth rate, and survival of piping plover chicks in New Jersey, USA. *Ecosphere* 12:e03782.
- U.S. Fish and Wildlife Service [USFWS]. 1985. Determination of endangered and threatened status for the piping plover. Final Rule. *Federal Register* 50:50726–50734.
- U.S. Fish and Wildlife Service [USFWS]. 1996. Piping plover (*Charadrius melodus*) Atlantic Coast population revised recovery plan. USFWS, Hadley, Massachusetts, USA.
- U.S. Fish and Wildlife Service [USFWS]. 2014. Biological Opinion and Conference Opinion Fire Island to Moriches Inlet, Fire Island Stabilization Project, Suffolk County, NY. USFWS, Hadley, Massachusetts, USA.
- Walker, K. M., J. D. Fraser, D. H. Catlin, S. J. Ritter, S. G. Robinson, H. A. Bellman, A. L. DeRose-Wilson, S. M. Karpanty, and S. T. Papa. 2019. Hurricane Sandy and engineered response created habitat for a threatened shorebird. *Ecosphere* 10:e02771.
- Weithman, C. E., J. D. Fraser, S. M. Karpanty, and D. H. Catlin. 2020. Relationship of current management practices to movements of piping plover broods in an Atlantic Coast population. *Journal of Field Ornithology* 91:170–188.
- Weithman, C. E., D. Gibson, K. M. Walker, S. B. Maddock, J. D. Fraser, S. M. Karpanty, and D. H. Catlin. 2018. Discovery of an important stopover location for migratory piping plovers (*Charadrius melodus*) on South Point, Ocracoke Island, North Carolina, USA. *Waterbirds* 41:56–62.
- Weithman, C. E., S. G. Robinson, K. L. Hunt, J. Altman, H. A. Bellman, A. L. DeRose-Wilson, K. M. Walker, J. D. Fraser, S. M. Karpanty, and D. H. Catlin. 2019. Growth of two Atlantic Coast Piping Plover populations. *Condor: Ornithological Applications* 121:duz037.
- West, G. B., J. H. Brown, and B. J. Enquist. 2001. A general model for ontogenetic growth. *Nature* 413:628–631.
- Westerkov, K. 1950. Methods for determining the age of game bird eggs. *Journal of Wildlife Management* 14:56–67.
- Whitfield, D. P. 2003. Density-dependent mortality of wintering dunlins *Calidris alpina* through predation by Eurasian sparrowhawks *Accipiter nisus*. *Ibis* 145:432–438.
- Wilcox, L. R. 1959. A twenty year banding study of the piping plover. *Auk* 76:129–152.
- Wilde, L. R., J. E. Simmons, R. J. Swift, and N. R. Senner. 2022. Dynamic sensitivity to resource availability influences population responses to mismatches in a shorebird. *Ecology* 103:e3743.
- Wiltermuth, M. T., M. J. Anteau, M. H. Sherfy, and A. T. Pearce. 2015. Habitat selection and movements of piping plover broods suggest a tradeoff between breeding stages. *Journal of Ornithology* 156:999–1013.
- Zeigler, S. L., B. T. Gutierrez, E. J. Sturdivant, D. H. Catlin, D. Fraser, A. Hecht, S. M. Karpanty, N. G. P. Id, and E. R. Thieler. 2019. Using a Bayesian network to understand the importance of coastal storms and undeveloped landscapes for the creation and maintenance of early successional habitat. *PLoS ONE* 14:e0209986.
- Zeigler, S. L., E. R. Thieler, B. T. Gutierrez, N. G. Plant, M. Hines, J. D. Fraser, D. H. Catlin, and S. M. Karpanty. 2017. Smartphone technologies and Bayesian networks to assess shorebird habitat selection. *Wildlife Society Bulletin* 41:666–677.
- Zuur, A. F., E. N. Ieno, and C. S. Elphick. 2010. A protocol for data exploration to avoid common statistical problems. *Methods in Ecology and Evolution* 1:3–14.

Associate Editor: Anthony Roberts.

SUPPORTING INFORMATION

Additional supporting material may be found in the online version of this article at the publisher's website.

How to cite this article: Robinson, S. G., K. M. Walker, H. A. Bellman, D. Gibson, D. H. Catlin, S. M. Karpanty, S. J. Ritter, and J. D. Fraser. 2022. Piping plover chick ecology following landscape-level disturbance. *Journal of Wildlife Management* e22325. <https://doi.org/10.1002/jwmg.22325>