esa ECOSPHERE

Adult piping plover habitat selection varies by behavior

Samantha Robinson,[1,2,†] Henrietta Bellman,[1,2] Katie Walker,[1] Daniel Catlin,[1] Sarah Karpanty,[1] Shannon Ritter,[1] and James Fraser[1]

[1]*Department of Fish and Wildlife Conservation, Virginia Tech, 310 W. Campus Drive, Blacksburg, Virginia 24061 USA*
[2]*Delaware Division of Fish & Wildlife, 6180 Hay Point Landing Road, Smyrna, Delaware 19977 USA*

Citation: 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(12):e03870. 10.1002/ecs2.3870

Abstract. Piping plovers (*Charadrius melodus*, "plover") are beach-nesting shorebirds that occupy their breeding range from about April to August. When plovers arrive on the breeding grounds, they select and defend territories, lay and incubate eggs, and tend to precocial broods; additionally, adults can return to a non-breeding stage after final nest failure or after chicks have fledged or died. We hypothesized that habitat selection would differ among these phases of the breeding cycle because the needs of the birds differ among them. We monitored plovers on Fire Island and Westhampton Island, New York, during 2016–2018, recording individual locations of adult birds. We used resource selection functions to determine whether breeding stage (pre-breeding, nesting, brooding, post-breeding), breeding status (breeding, non-breeding), or instantaneous behavior class (parental [incubating, brooding, and accompanying chicks], non-parental [all other behaviors]) best explained relationships with landscape characteristics known to be important to breeding plovers. Differences in habitat selection between adults exhibiting parental behaviors and non-parental behaviors had the greatest support in our model set. Compared with non-parental plovers, plovers displaying parental behavior selected areas closer to bay intertidal habitats and with proportionally more dry sand in the surrounding landscape than other habitat types. Non-parental plovers avoided areas with more dry sand and did not select for or against bay intertidal habitats. Additionally, non-parental plovers avoided development and higher elevation areas more than parental plovers, although both exhibited avoidance of these features. The total amount of suitable habitat ranged from 100.14 ha to 151.07 ha. In each year, there was more suitable habitat for parental plovers (129.57–151.07 ha) than non-parental plovers (100.14–108.83 ha). Due to these differences, when improving, creating, and protecting plover habitat, managers should consider habitat needs of both behavioral classes. Habitat management for nesting and brooding plovers should focus on maintaining vegetation-free sand and access to foraging habitat, and habitat management for non-parental plovers should focus on flat, low-elevation foraging habitats, particularly areas further from development.

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

Received 3 May 2021; revised 26 July 2021; accepted 5 August 2021. Corresponding Editor: Brooke Maslo.

† **E-mail:** samgr@vt.edu

Introduction

Habitat conservation practices should be built on complete knowledge of animals' habitat selection patterns, especially when managing imperiled species (Caughley 1994, Jones 2001). Recent authors have highlighted the importance of full life cycle studies (Hostetler et al. 2015, Marra et al. 2015) arguing that conditions in one part of an individual's or species' range can affect

survival and/or reproduction during another part of the life cycle. However, even within one part of the range or life cycle, requirements of individual animals may vary. Therefore, the choices that animals make on the landscape may be dictated by several co-occurring factors. In some studies, explanatory variables that relate to a different part of the life cycle may be included in a single life stage analyses, such as using information on young-rearing habitat on nest studies (Walker et al. 2019). While this often produces satisfactory results, a deeper understanding of animal ecology and conservation may be obtained by more explicitly breaking down resource needs by the various stages of daily life. For instance, habitat use or selection may differ between life stages, such as when individuals are actively rearing young vs. preparing for migratory departure. Furthermore, depending on the degree of difference among life stages, biological stage-specific habitat needs may have differing importance to the annual cycle (Ahlering and Faaborg 2006). However, specific behaviors, rather than biological (breeding) stage, may dictate habitat selection, and thus, the two concepts should be compared and contrasted for a thorough understanding of wildlife response to landscape processes (Lima and Zollner 1996). By determining how habitat selection may vary among life cycle stages, resource managers can protect optimal habitat at ideal times, and marginal habitat can be targeted for management.

In dynamic systems, habitat conditions can rapidly change within and between years, particularly in disturbance-dependent systems where a single event can cause widespread and long-lasting change (Ray and Gregg 1991, Walker and Schlacher 2011, Walker et al. 2019). Barrier islands, typically long sandy islands that lay adjacent to the mainland (Leatherman 1988), are dynamic within and between years. Within years, vegetation increases during the growing season, and between years, island geomorphology changes from storm events and tidal energy (Bellman 2018). Species occupying dynamic landscapes may then modify how they interact with the landscape in response to within- or between-year temporal or spatial cues (Boulinier and Danchin 1997, Doligez et al. 2002).

The piping plover (*Charadrius melodus*; plover), a federally protected species, inhabits disturbance-dependent environments (Hunt et al. 2018, Robinson et al. 2019). Plovers are migratory and interact with these landscapes in varying ways among breeding, migratory, and wintering sites (Haig and Oring 1985, Fraser et al. 2005, Cohen et al. 2008*a*, Weithman et al. 2018). On the breeding grounds, plovers transition through a variety of stages, viz., territory establishment and courtship, initiating and incubating nests, tending to chicks, and preparing for southward migration (Elliot-Smith and Haig 2004). Because of different biological and spatial requirements within these stages, such as needing nest sites that are adequately camouflaged, foraging habitat that is accessible for flightless chicks, or mudflats with abundant prey following and prior to migration (Flemming et al. 1992, Maslo et al. 2019, Walker et al. 2019), plovers likely select habitat differently among stages. However, across all breeding stages, adult plover behavior also changes within stage. For example, nesting and brooding adult behavior likely varies between when they are tending to their nests or chicks and when foraging, as one adult typically forages separately and elsewhere (Cairns 1982, Elliot-Smith and Haig 2004). Plover habitat management may be improved by better understanding how plover adults use habitat types between breeding stages or behavioral states.

Plovers nest on Fire Island and Westhampton Island (hereafter; Fire Island), barrier islands off the south shore of Long Island. Hurricane Sandy broadly affected Fire Island in the fall of 2012, causing widespread habitat change on plover breeding grounds. In the approximately 15 yr preceding Hurricane Sandy, plover habitat primarily was relatively narrow, oceanfront sand, backed by vegetated dunes (Walker et al. 2019, Zeigler et al. 2019). During Hurricane Sandy, much of the beachfront was eroded (Hapke et al. 2013), but some beachfront and dune sand was transferred to overwash fans, creating wide swaths of sand that extended across the width of the island (Walker et al. 2019). Widespread overwash creation across portions of the island facilitated comparison of plover habitat selection and suitability across a habitat gradient. Due to the additional habitat formation, the plover population on Fire Island increased considerably between 2016 and 2018, from 36 to 58 pairs (Walker et al. 2019). The population increase was

coincident with a change in habitat selection from birds nesting on narrow oceanfront beaches to wider overwashes following aforementioned changes in landscape condition (Walker et al. 2019).

Much of the existing habitat selection studies for plovers is nest-site selection studies, or spatially implicit (i.e., without using actual locations of individuals, Le Fer et al. 2008, Maslo et al. 2016, Walker et al. 2019). Fine-scale selection studies have shown that nesting plovers select for areas with <20% vegetation cover, and areas of wide beach width (Maslo et al. 2011). Shell cover, distance to dune, amount of wrack, and distance to vegetation also have been significant predictors of plover nest locations (Burger 1987, Flemming et al. 1992, Boyne et al. 2014). Nest-site selection, however, does not describe all plover habitat requirements at the breeding grounds, including habitat selection before and after nesting (Cairns 1982, Cohen and Fraser 2010). Habitat selection can change between life stages due to different food requirements, foraging ability, movement ability, risk of predation, or thermoregulation ability (Moermond 1979, Paasivaara and Pöysä 2008, Bloom et al. 2013). Unlike pinpointing stationary nest locations, obtaining accurate locations of piping plovers is challenging due to efforts to reduce disturbance and a lack of fine-scale technology to mark a large sample of individuals. Previous studies of adult plover or chick habitat selection have illustrated that plovers benefit from areas of low human use, allowing individuals to focus on foraging and resting rather than being alert (Burger 1994, DeRose-Wilson et al. 2018), and avoid areas with higher predation risk such as cliffs and trees (Anteau et al. 2014). Plover chick habitat selection suggests that moist and saturated habitats are more important for foraging than dry or densely vegetated habitats, and dunes (Le Fer et al. 2008, Stantial 2020). Because of these differences, habitat selection analyses should consider more nuanced adult plover habitat selection throughout the breeding season to ensure that all suitable habitat is considered for management and conservation (Paterson et al. 2012).

Since biological requirements and constraints differ among breeding stages, we hypothesized that habitat selection also might differ. Alternatively, habitat selection may reflect differences in behavior, as breeding adults may not be consistently tending to nests or chicks (Flemming 1987, Schneider and McWilliams 2007) and whether relationships with the landscape change over time. Our objectives were to (1) determine whether breeding stage or instantaneous behavior better predicted adult plover habitat selection, (2) predict suitability of available habitat based on breeding stages or behavior, and (3) estimate if the amount of available suitable habitat differed among stages/behaviors. We predicted that breeding stage, rather than behavior, would best predict habitat selection, as adults likely do not stray far from their breeding territories even when not actively tending chicks. We predicted that habitat selection of pre-breeding and nesting adults would be similar. When birds arrive on the breeding grounds, they begin defending territories and creating potential nest sites (Cairns 1982). Therefore, based on past studies, we predicted that adults in these stages would select for areas of open, sparsely vegetated sand to increase camouflage and reduce detection of nests and chicks by terrestrial predators (Troscianko et al. 2016). We also predicted that brooding adults would select areas closer to intertidal foraging habitats, particularly low-energy intertidal habitats that are ideal for brood foraging (Elias et al. 2000), and that post-breeding adults would select areas closer to both high- and low-energy foraging habitats to increase fat reserves prior to departing for migration (Lindström and Piersma 1993). Further, we predicted that adults would select against steeper slopes, as steeper areas may have lower invertebrate abundance, and also may be more difficult to traverse, particularly for plover chicks. Finally, we predicted that suitable habitat would decrease between 2016 and 2018, as vegetation increased (Bellman 2018).

Material and Methods

Study area

We studied plovers on a 27-km stretch of Fire Island and Westhampton Island, New York, 2016–2018 (Fig. 1). The study area consisted of Fire Island National Seashore, managed by the National Park Service, Smith Point, and Cupsogue Beach County Parks, managed by Suffolk

County Parks, and Robert Moses State Park, managed by New York Parks, Recreation, and Historic Preservation. At Fire Island National Seashore, monitoring was only conducted at the Fire Island Lighthouse Beach, and the Otis Pike Wilderness Area (Fig. 1). These islands are bounded by the Atlantic Ocean to the south and several bays to the north (Fig. 1). Habitat types in the study area consisted of oceanfront sandy beaches, dunes, overwashes (areas where storm water carried sand landward over the island), bayside sandy beaches, ephemeral pools, and filled Hurricane Sandy breaches (Walker et al. 2019). The study area also included three inlets, Fire Island Inlet, Old Inlet, and Moriches Inlet. Hurricane Sandy storm surges created Old Inlet at a location in the Fire Island National Seashore where a previous inlet had been closed for decades. Fire Island and Moriches inlets are dredged inlets, stabilized with jetties to the east and west. Prior to the 2015 plover breeding season, two restoration areas were built by the U.S. Army Corps of Engineers (USACE) to create plover nesting habitat as mitigation for island stabilization efforts, one at the eastern end of Smith Point County Park ("Great Gun," 34.8 ha), and one in the middle of Smith Point County Park ("New Made," 6.6 ha; Bellman 2018, Walker et al. 2019). Human use was variable among management areas and comprised pedestrian and off-road vehicle use, with boat access along the shoreline (DeRose-Wilson et al. 2018). Dominant vegetation included American beachgrass (*Ammophila breviligulata*), common reed (*Phragmites australis*), seaside goldenrod (*Solidago sempervirens*), and woolly beachheather (*Hudsonia tomentosa*). Fire Island also supports coniferous and deciduous tree communities, and poison ivy (*Toxicodendron radicans*) thickets, but these were not within plover breeding areas.

Field methods

We surveyed beaches for plovers April–August during 2016–2018 (DeRose-Wilson et al. 2018, Walker et al. 2019, Weithman et al. 2019). We searched for nests using behavioral cues and by walking through plover habitat. We trapped adults at nests using drop traps (Wilcox 1959) and banded adults using either uniquely identifiable 4-color band combinations on the tibiotarsus or a uniquely coded alphanumeric flag opposite a color band on the tibiotarsus (Roche et al. 2014). We confirmed adult plovers as breeders by trapping them on nests or by confirming incubation using 20–60× spotting scopes.

We surveyed for banded adults and chicks every 1–3 d by walking transects, approximately 100–300 m apart, parallel to the shoreline. We assigned a behavior to each adult based on observed behavior at first encounter and later classified all behaviors into two categories: parental and non-parental. Parental behaviors included incubating nests, broken wing displays, defensive peeping, and brooding or attending to chicks, whereas non-parental behaviors included foraging, aggression, territorial, roosting, loafing, and courtship. We also recorded disturbed as a behavior, which indicated a plover was reacting to researcher's presence prior to initial observation. We omitted disturbed locations from analyses because they were researcher-induced behaviors. We recorded individual locations of birds with coordinate geometry by first recording an observer's location using a Trimble GPS unit (Trimble Geospatial, Sunnyvale, CA, USA) and offsetting that location with an azimuth from a compass and a distance from a Nikon 8397 Aculon Laser Rangefinder (Nikon, Minato, Tokyo, Japan; Robinson et al. 2020*a*).

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

Using adult movement to define scales

Adult plover habitat selection may vary among spatial scales because adults are highly mobile and likely perceive resource availability at multiple scales. For example, plovers may evaluate foraging habitat at fine scales due to local invertebrate abundance but may evaluate vegetation at broader scales to avoid predator encounters. Therefore, habitat selection studies should address questions of whether the scale of relationships varies among landscape predictors via scale optimization (Boyce 2006, McGarigal et al. 2016). To determine the potential scales at

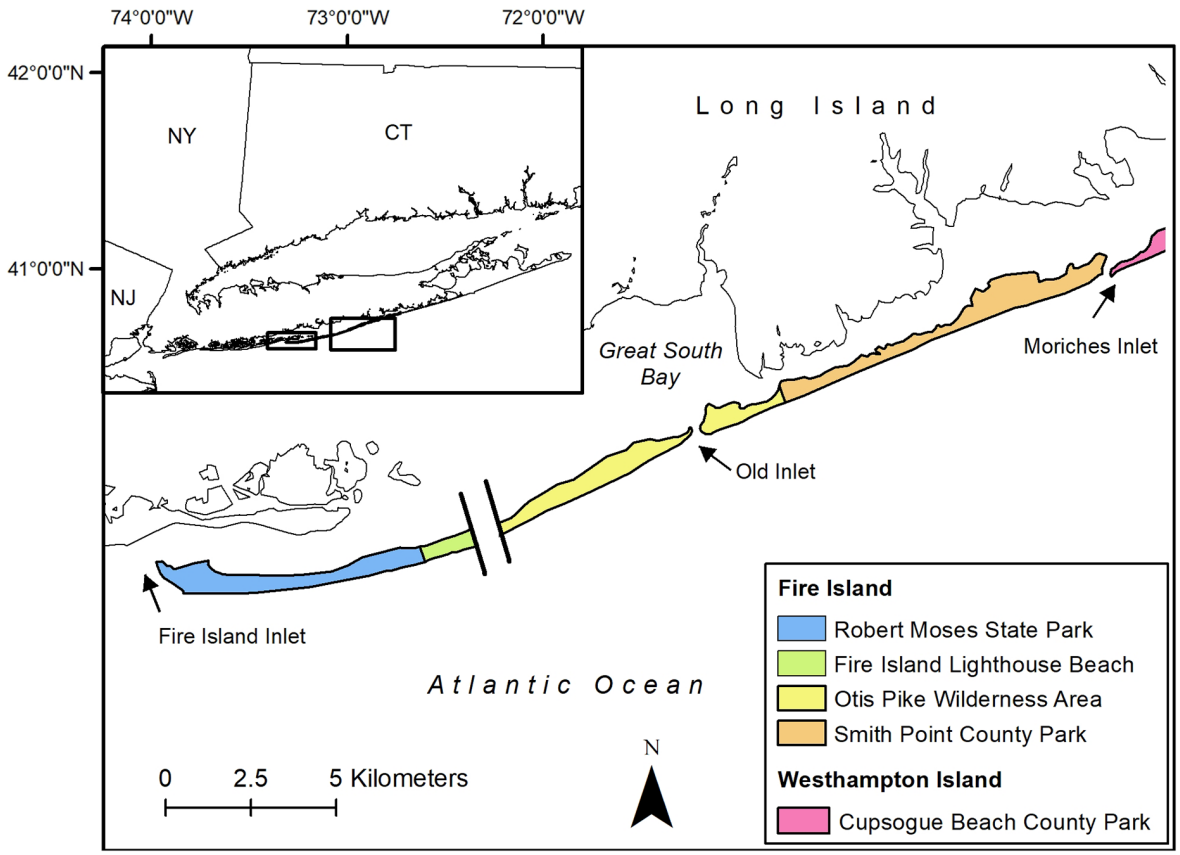

Fig. 1. Study area on Fire Island and Westhampton Island, New York, in which adult piping plovers were located during 2016–2018 and resource selection functions were created to understand habitat selection of adult piping plovers between breeding stages or behavior classes. Lines separating the Fire Island Lighthouse Beach from the Otis Pike Wilderness Area represent a portion of Fire Island not surveyed for this study.

which adult plovers selected for each habitat variable, we used plover movement data to define radii of circles within which we summarized habitat data for use in resource selection functions (McGarigal et al. 2016). When we recorded >1 location of an individual in a day, regardless of breeding status, we estimated the daily average and median distance that individual moved using all observations from that day. We also estimated the average and median distance between subsequent daily observations of individuals, regardless of breeding stage. Finally, using birds only in the nesting stage, we estimated the mean distance birds were observed from their nest. Because we had no prior knowledge about selection scale in adult plovers, we used all potential movement values as circle radii, to not rule out any potential scale relationships. We also used 5 m and 10 m, the mean and maximum error in the location data collection (Robinson et al. 2020*a*).

Image classification

Imagery and LiDAR were collected by aircraft between February and April 2016–2018 (Axis Geospatial, Easton, MD, USA). We classified annual fine-scale (15 cm) imagery into four classes (dry sand, wet sand, vegetation, and water), using maximum-likelihood classification in ArcGIS 10.6 (ESRI Inc., Redlands, CA, USA). We manually interpreted and digitized development in our study area (i.e., parking lots, buildings, roads, jetties, boardwalks) and incorporated development into the classification as a fifth land-cover class. We created a digital elevation model (DEM) using LiDAR from each year.

As the timing of aerial imagery did not always correspond with low tide, we used the DEM to identify intertidal areas. The oceanfront intertidal range was 0–1.2 m in elevation, based on the highest astronomical tide at NOAA Moriches Inlet tidal station, and the bayside intertidal range was 0–44.50 cm, based on mean high water at the NOAA Smith Point Bridge tidal station (NOAA 2017). We reclassified each DEM to select pixels within both the oceanfront and bayside intertidal and subtidal range. These pixels were reclassified to represent intertidal wet sand and water, respectively. The refined layers from each of these methods were superimposed over the classification.

Variables

From our 15-cm land-cover classifications, we created several 1-m raster layers using the land-cover classifications to evaluate specific hypotheses, as 1 m was the error of our GPS units (Robinson et al. 2020*a*). Classification accuracy at this resolution ranged from 86.87% to 90.5% among years. To understand selection for foraging habitat, we created distance-based raster layers, measured in meters, for Euclidean distance to ocean, Euclidean distance to bay, least-cost distance to ocean, and least-cost distance to bay. We also created layers for Euclidean distance to development and Euclidean distance to vegetation. Development in the study area, in addition to representing human disturbance, could represent areas in which avian and mammalian predator species congregate in search of anthropogenic waste, such as discarded food (Black 2021). Potential predators of plovers that may be influenced by development or vegetation include avian predators such as herring gull (*Larus argentatus*), great black-backed gull (*L. marinus*), American crow (*Corvus brachyrhynchos*), and fish crow (*C. ossifragus*). Mammalian predators included red fox (*Vulpes vulpes*), raccoon (*Procyon lotor*), and feral cat (*Felis catus*). For distance rasters, each pixel in a raster had a single value that represented the distance from that cell to a landscape feature of interest. Least-cost distance rasters represented the minimum walking distance to a feature assuming water and vegetation are movement barriers for flightless chicks (Walker et al. 2019). We created Euclidean distance layers using the Euclidean distance tool in ArcGIS and least-cost distance layers using the Path Distance tool. We used the DEM to evaluate selection for elevation. High elevation areas are more likely to be dry and thus have lower invertebrate abundance (Elias et al. 2000, Cohen et al. 2009). High elevation areas in our study area, such as high dunes (~11 m high), also may increase susceptibility to aerial predation due to improved detectability by predatory birds in flight. Finally, we derived a slope layer from the DEM, using the Slope tool in ArcGIS.

We generated five times as many random points as adult locations to represent available habitat for plovers (Cooper and Millspaugh 2001). Because detection probability of plovers is likely low in vegetation, and because plovers primarily use sandy habitats, we constrained used and random points to wet and dry sand pixels. Within circles with radii of each potential selection scale, we averaged all pixel values of each variable for the adult plover locations and random locations using the "extract" function in the *raster* package in R (Hijmans 2016, R Core Team 2018). In each circle, we also calculated the proportion of dry sand and vegetation pixels, as areas with more dry sand and less vegetation are likely to reduce plover detection by predators because plovers are camouflaged in sand. We used both the proportion of vegetation and distance to vegetation, as distance to vegetation represents the distance to any vegetation, even small patches, whereas areas with a greater proportion of vegetation indicate an area of denser vegetation cover. To compare effect sizes among predictor variables, we standardized all continuous variables using the mean and standard deviation.

Scale optimization

As habitat selection is a multi-scale process and landscape features may be evaluated by plovers at different scales, we used scale optimization to determine the most relevant scale at which adult plovers selected each variable. We developed separate model sets for each landscape variable. In a model set, each scale identified by the adult movement analysis was a predictor variable in univariate resource selection functions (Chambers et al. 2016, McGarigal et al. 2016, Timm et al. 2016). We ranked each model in a set by AICc, selecting the best-supported scale with ≤2 AICc. If there was not one clearly

supported scale, we selected the smallest scale with ≤2 AICc based on adult plovers being relatively small, thus likely making choices at fine scales (Miguet et al. 2016). We tested for correlation among the final set of predictors at their selected scales. To reduce spatial autocorrelation, we spatially rarified the data by removing locations in each breeding stage, year, and type of point (used or random) within 5 m of all other points using the SDMtoolbox for ArcGIS 10.6 (Brown et al. 2017).

Analytical methods

We evaluated habitat selection of breeding adult piping plovers in the study area on Fire Island and Westhampton Island, New York (Fig. 1). Based on our hypotheses of whether behavior or breeding stage better explained adult habitat selection, we assigned each adult location a breeding stage and behavior for three categorical predictor groups. The first grouping classified adults by breeding stage: pre-breeding, nesting, brooding, and post-breeding. Adults were nesting if observed between the time of nest initiation and nest hatch or failure. Adults were brooding if observed between nest hatch and the last time a brood was observed alive or 25 d post-hatch. If observed prior to nest initiation or following nest failure, brood failure, or brood fledging, we categorized adults as pre-breeding and post-breeding, respectively. If an individual nested more than once, we removed locations between nesting attempts. Adults during this period may exhibit different habitat selection, but we did not have a sufficient sample to analyze this stage separately.

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

We randomly subset our adult locations and random points into a training set (75%) and a testing set (25%) to evaluate the accuracy of our predicted model. All RSF models were built using the training set. We evaluated fixed-effects logistic regression models with additive or interactive effects of all our predictor variables at the best-supported scale from the adult movement analysis, with either adult breeding stage, breeding status, or behavior class, and year. We evaluated all models against a base model that included all landscape variables but did not include year, breeding stage, breeding status, or behavioral class. The model set included 15 models, and we ranked models using AICc. We considered all models ≤2 ΔAICc to be competitive (Burnham and Anderson 2002). We evaluated resource selection and habitat suitability based on the adult grouping (i.e., breeding stage, breeding status, behavior) in the best-supported model. We used the "roc" function in package *pROC* in R to determine area under the curve (AUC), the overall predictive ability of the model (Robin et al. 2011).

Creation of suitable habitat layer

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

We validated predicted habitat suitability using the 25% subset of used and random points

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

To evaluate the total amount of suitable habitat annually, we determined a suitability threshold for each year-class (e.g., 2016-parental) combination using the minimized difference threshold (MDT; Jiménez-Valverde et al. 2013), where the difference between sensitivity (true positive rate) and specificity (true negative rate) was calculated for each possible suitability threshold (1–100). The cutoff value that represents the smallest difference between sensitivity and specificity is the selected threshold. Using this value, any predicted suitability value on the predicted raster above the threshold would be suitable, and any value below the threshold would be unsuitable. We used the 25% training point subset to evaluate how well the suitability layer predicted adult plover use points by determining the proportion of plover points in suitable habitat. Finally, we summed the binary predicted suitability layers from each year for an ensemble layer to visualize where habitat suitability agreed or differed between or among the best-supported grouping scheme.

Results

We recorded 2889 adult locations during 2016–2018 from 172 breeding individuals. After assuring a minimum of 5 m between locations within location type, year, and breeding stage, we had 2060 adult plover observations. Of these locations, 19.9% were pre-breeding, 40.2% were nesting, 29.4% were brooding, and 10.5% were post-breeding. For behavior class, 42.1% were breeding and exhibiting parental behaviors, and 57.9% were exhibiting non-parental behaviors.

Selection scales

Based on the movement of adult plovers, we used seven circle sizes in which to evaluate selection for different habitat attributes (Table 1). We used 106 and 344 m, as these were the median and mean distances adult moved when the time between subsequent observations was one day. We used 87 and 211 m, as these were the median and mean distances between adult locations within a day. Finally, we used 150 m as this was the average distance adults in the nesting stage were observed from their nest (Table 1). When evaluated in univariate model sets for each variable, plover habitat selection was generally operating at larger scales. However, selection for least-cost distance to ocean, slope, dry sand proportion, and vegetation proportion was

Table 1. Potential scales tested for resource selection of habitat by adult piping plovers on Fire Island and Westhampton Island, NY, 2016–2018.

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

Note: Scales were evaluated for each landscape variable and ranked by AICc in univariate logistic regression models (Appendix S1).

† Robinson et al. (2020*a*).

occurring at scales <100 m (Table 1, Appendix S1: Tables S1–S10). Despite being evaluated at different scales, Euclidean and least-cost distance to ocean intertidal and Euclidean and least-cost distance to bay were correlated ($r = 0.79$ and 0.84, respectively). We continued modeling efforts with the two least-cost distance variables. Although we were modeling selection of adults that could fly, and thus could reasonably reach any ocean or bay intertidal habitat, adults tending broods were limited by habitat availability for their chicks and were unlikely to fly to areas their chicks could not access.

Resource selection

A single model, the interactive model in which habitat selection was best described by behavioral group (parental vs. non-parental), but not by year, held 85% of the weight in model selection (Table 2). This model was reasonably predictive with an AUC of 0.77 (95% CI 0.75–0.79). Nearly all land-cover variables were influential to plover habitat selection at their top selected scale (Fig. 2, Appendix S1: Table S11).

Plovers in both parental and non-parental behavior classes avoided areas with more vegetation, but they selected sites at lower grades and areas closer to ocean intertidal habitat (Fig. 3). Selection also differed between behavior classes, such that non-parental plovers avoided areas with greater proportions of dry sand relative to random points, whereas parental plovers selected areas with higher proportions of dry sand (Fig. 4). Parental plovers selected for areas at higher elevation than non-parental plovers, but overall, lower elevations were favored compared to random points for both behavioral groups (Fig. 4). Parental plovers selected areas closer to the bay intertidal whereas non-parental adult plovers did not select habitat relative to the distance to bay intertidal (Fig. 4). Birds in both behavior classes also selected for sites farther from development, although the magnitude of the effect was greater for non-parental adults (Fig. 4).

Mapping

The mapping schemes that used 5 equal-area visualization classes were more predictive than 10 equal-area visualization classes for every predictive raster made. Predictive accuracy with 5 visualization classes using our 25% training sample ranged from 0.83 to 0.93 (Table 3).

Table 2. Model selection table to assess differences in resource selection for adult piping plovers on Fire Island and Westhampton Island, NY, 2016–2018.

Model	K†	ΔAICc	w_i‡	Log likelihood
Predictors × Behavior	18	0.00	0.85	−3898.07
Predictors × Behavior × Year	54	3.42	0.15	−3863.53
Predictors × Breeding Stage	36	50.05	0.00	−3905.00
Predictors × Breeding Status	18	66.52	0.00	−3931.33
Predictors × Breeding Stage × Year	108	67.59	0.00	−3840.75
Predictors × Breeding Status × Year	54	69.13	0.00	−3896.38
Predictors × Year	27	74.13	0.00	−3926.09
Predictors + Breeding Status + Year	12	76.92	0.00	−3942.55
Predictors + Year	11	77.95	0.00	−3944.07
Predictors + Behavior + Year	12	78.68	0.00	−3943.43
Predictors + Breeding Stage + Year	14	79.46	0.00	−3941.81
Predictors + Breeding Status	10	82.14	0.00	−3947.16
Predictors	9	83.01	0.00	−3948.60
Predictors + Breeding Stage	12	83.52	0.00	−3945.85
Predictors + Behavior	10	83.93	0.00	−3948.06

Notes: Differences evaluated were between breeding stage, behavior, and year. Breeding stage indicates that adult locations were split into four classes, pre-breeding, nesting, brooding, and post-breeding. Breeding status indicates that adult locations were split into two classes based on whether adults were breeding (nesting or brooding) or not (pre- or post-nesting). Behavior indicates that adult locations were split into two classes based only on behavior, parental, and non-parental. Predictors included elevation, slope, least-cost distance to ocean intertidal, least-cost distance to bay intertidal, distance to vegetation, distance to development, proportion of dry sand around points, and proportion of vegetation around points.

† Number of parameters.

‡ Model weight.

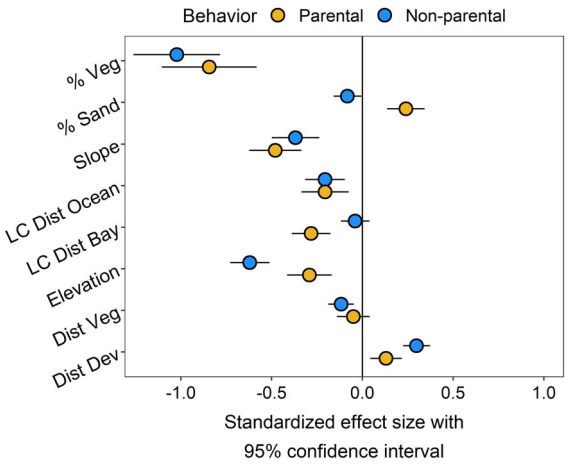

Fig. 2. Standardized effect size for top ranked logistic regression resource selection function describing breeding adult piping plover habitat selection on Fire Island, New York. For distance variables, a negative effect suggests selection closer to the feature, and for proportion variables, a positive effect suggests selection with more of the feature within the specified buffer. On the vertical axis, % Veg stands for the amount of vegetation within 10 m of locations, % Sand is the amount of dry sand within 5 m of locations, and "LC Dist Ocean" and "LC Dist Bay" represent the least-cost distance to ocean or bay, respectively, or the distance to walk to ocean or bay intertidal habitats, avoiding vegetation or water. "Dist Veg" represents the straight-line distance to vegetation, and "Dist Dev" represents the straight-line distance to development.

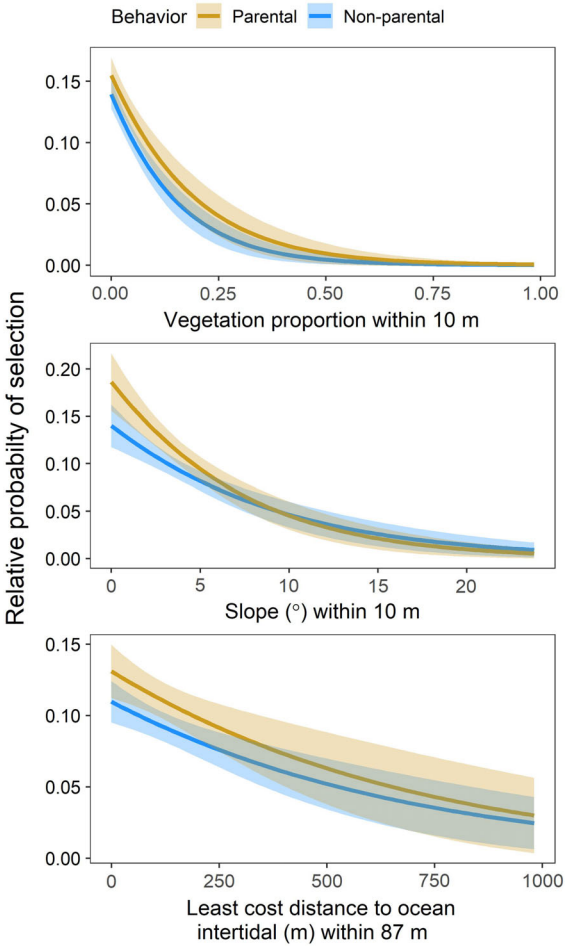

Fig. 3. Three variables from a logistic regression resource selection function assessing habitat selection of adult piping plovers on Fire Island, New York, which signified similar relationships between adults behaving parentally and adults exhibiting all other behaviors. Lines represent the relative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

Binary suitability thresholds (suitable vs. not suitable), as determined by the MDT ranged from 0.18 to 0.19. Therefore, predicted suitability below 0.18–0.19 was considered unsuitable, and above was considered suitable. During 2016–2018, there was more suitable habitat for parental adults (28–34% of sand) than non-parental birds (22–23% of sand; Table 3). Suitable habitat only encompassed 60–72% of parental locations and 66–73% of non-parental locations, suggesting the model was predicting some used habitats to be unsuitable (Table 3). The amount of suitable habitat ranged from 100.14 to 151.07 ha, declined an estimated 21.5 ha for parental plovers between 2016 and 2018, and increased an estimated 8.5 ha for non-parental plovers between 2016 and 2018.

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

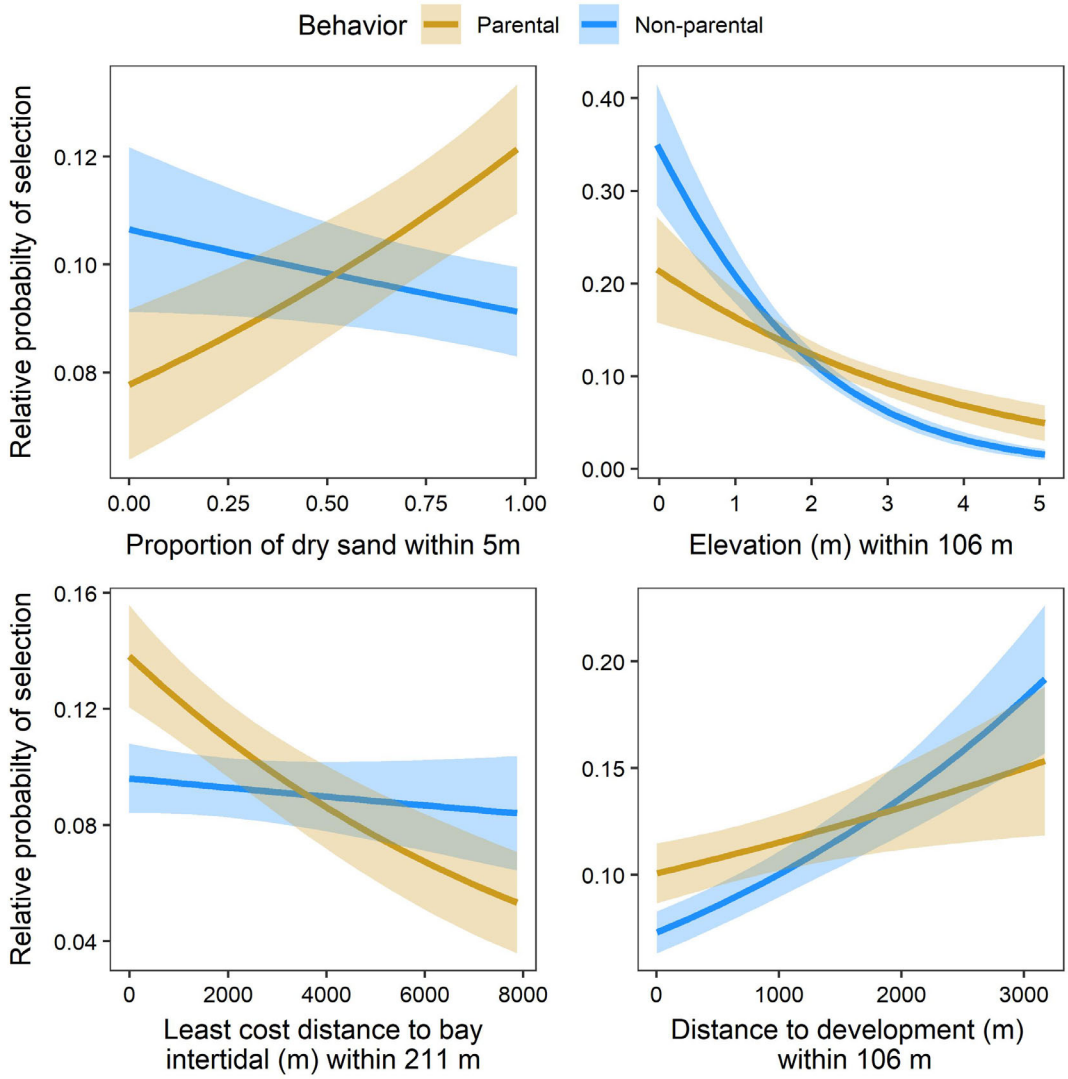

Fig. 4. Four variables from a logistic regression resource selection function, assessing habitat selection of adult piping plovers on Fire Island, New York, which signified differences between adults behaving parentally and adults exhibiting all other behaviors. Lines represent the relative predicted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

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

		Suitable habitat		Correlation		
Behavior class	Year	Proportion	Area (ha)	5-bin	10-bin	Proportion used points suitable
Parental	2016	0.34	151.07	0.89	0.85	0.68
Non-parental	2016	0.22	100.14	0.83	0.75	0.73
Parental	2017	0.34	149.57	0.90	0.82	0.60
Non-parental	2017	0.23	100.66	0.88	0.84	0.67
Parental	2018	0.28	129.57	0.93	0.85	0.72
Non-parental	2018	0.23	108.83	0.88	0.85	0.66

Notes: The proportion of habitat suitable was the proportion of the pixels for with predicted values above 0.18–0.19, depending on the year and behavior class, and hectares of suitable habitat was the total area of that proportion.

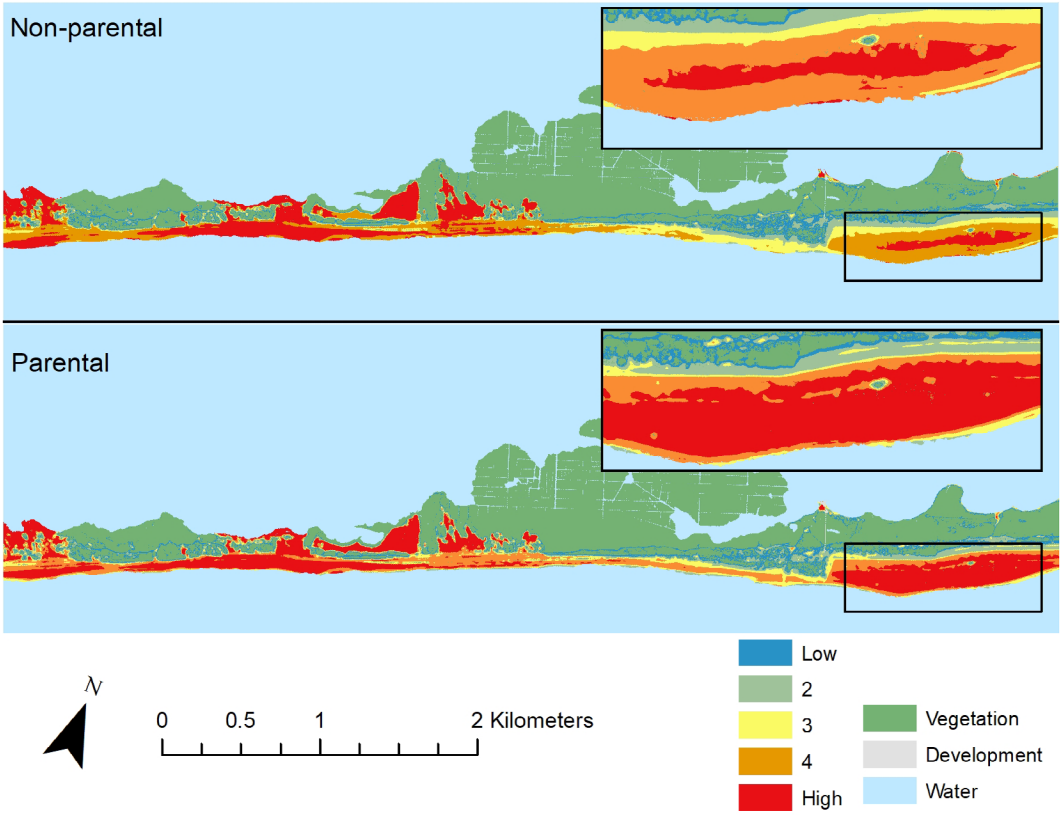

Fig. 5. Adult piping plover predicted habitat suitability maps for birds exhibiting non-parental behaviors (top) and parental behavior (bottom) on Fire Island, New York, in 2016. The resource selection function was predicted onto dry and wet sand classified from 2016 aerial imagery and land-cover classifications. Each visualization class (1–5) was the range of probability values that allowed for an equal number of pixels among all classes, (i.e., 20% of dry sand pixels for each class). In the legend, low (blue) represents the lowest 20% of predicted suitability values, and high (red) represents the highest 20% predicted suitability values. Zoom insets show differences in suitability at the Great Gun restoration area.

suitable for parental plovers than non-parental plovers. The larger USACE restoration area (Great Gun) mapped as suitable for both behavior groups, although more suitable for parental plovers, whereas the smaller restoration area (New Made) mapped as highly suitable for both behavior classes. From the ensemble layer in each year, 16.1–19.6% of the sand in the study area was suitable for at least one behavioral class, and 17.1–19.1% was suitable for both behavioral classes (Fig. 6).

Discussion

For several habitat variables, parental adult plovers selected habitat differently than non-parental plovers. Specifically, parental plovers selected for areas with more dry sand, closer to bay intertidal habitats, at higher elevations and closer to development than non-parental adult plovers. Furthermore, on Fire Island and Westhampton Island there was more suitable habitat for parental plovers than for plovers exhibiting other behaviors. This divide in selection demonstrates that we should not only evaluate habitat suitability using stationary or spatially implicit data, but instead we should consider selection across life stages for a holistic assessment of habitat requirements and management.

The strongest predictor of habitat selection for both behavioral classes was the amount of vegetation within 10 m of sand pixels. Determining

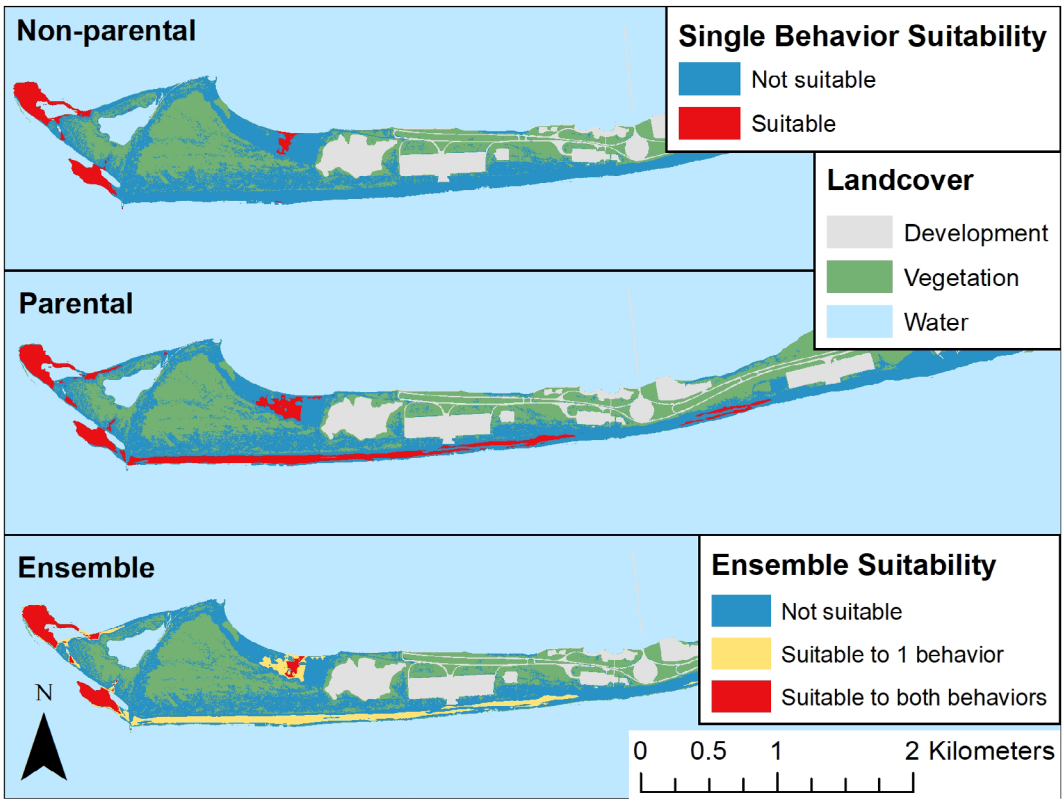

Fig. 6. Suitable vs. non-suitable sand for piping plovers on Fire Island, New York, in 2016 divided into non-parental piping plovers (top), parental plovers (middle), and an ensemble of both non-parental and parental plovers (bottom). Resource selection functions were predicted onto 2016 aerial imagery and land-cover classifications. To be "suitable," the predicted suitability value was above 0.18–0.19, depending on the year and behavior class.

use thresholds and identifying avoidance of certain sized vegetative patches can assist managers in designing or modifying landscapes to best suit the habitat needs of species (Huggett 2005). At the 10-m scale, the relative probability of selection for parental and non-parental adults was nearly zero at 50% vegetation cover. Therefore, this may be a threshold at which vegetation becomes too dense for plovers to move through and becomes a liability for plovers, perhaps due to predator concealment. Past studies illustrated that plovers readily use sparsely vegetated habitats, even occasionally placing their nest right next to, roosting under, or gleaning insects off of vegetation (Burger 1987, McGowan et al. 2007, Cohen et al. 2008*b*). Our results illustrate that plovers do not avoid all vegetation, as parental plovers neither selected for or against areas close to vegetation. In sparsely vegetated habitat, the distances to small patches of vegetation are likely to still be small, and thus, adults primarily may be avoiding areas with extensive dense vegetation cover. Fifty percent vegetation within 10 m —the scale at which we summarized relative vegetation density—would represent a 160-m^2 patch of vegetation, or multiple patches totaling 160 m^2. Managers could use this level of vegetation as a target size to remove vegetation patches in nesting plover areas, or when vegetation is more than sparse.

Similarities in selection between behavioral classes also were apparent for slope and least-cost distance to ocean intertidal. Selection for areas closer to the ocean intertidal and with lower slopes likely represents the importance of foraging habitat for adult plovers (Fraser et al.

2005, Cohen et al. 2009). If, for example, a particular area is close to the ocean, but the slope is steep, it may not have abundant or accessible marine invertebrate prey in the intertidal zone (Jaramillo et al. 1993).

Avoidance of areas with less surrounding vegetation around them likely represents predator avoidance by plovers. Similarly, avoidance of developed areas such as parking lots or buildings may reflect strategies to avoid predators that are attracted to human food at waste disposal sites. Avoidance of development also could be a strategy to reduce exposure to human disturbance, since anthropogenic disturbance can be negatively correlated with plover chick survival (DeRose-Wilson et al. 2018) and adult survival (Gibson et al. 2018). While both behavioral classes avoided development in our study, the magnitude of development avoidance was greater for non-parental adults than parental adults. This difference may be related to specific sites selected by post-breeding birds, particularly the areas surrounding the new inlet created by Hurricane Sandy that supported approximately 30% of adult post-breeding locations. The new inlet (Old Inlet; Fig. 1) is approximately 2 km from the nearest human development and is part of the National Wilderness Preservation System (Dietz et al. 2015), which reduces or eliminates human and vehicle traffic. Thus, it may be attractive to plovers fueling for migration without being disturbed.

A lack of selection for bay intertidal habitats by non-parental plovers was surprising. Bay intertidal habitats tend to have greater invertebrate abundance than ocean intertidal habitats (Loegering and Fraser 1995, Cohen et al. 2009, DeRose-Wilson et al. 2018), and many non-parental birds exhibited foraging behaviors (approximately 40%). That post-breeding plovers congregated at Old Inlet was notable given that there was no access to low intertidal bayside foraging habitat. Instead, the inlet and ocean intertidal habitats accreted following Hurricane Sandy as the land surrounding the inlet began to migrate. Consequently, foraging quality in these areas may have been similar to some bay areas because it was relatively low wave energy (Elias et al. 2000). This site also is adjacent to disconnected flood shoals, submerged sandbars that emerge at low tides, which were not included in this analysis but likely contributed to the use of Old Inlet by non-breeding adults. Non-parental adults, particularly post-breeding, foraged at flood shoals at low tide and roosted around the inlet at high tide.

On average, non-parental adults were about 400 m farther from the bay compared with parental adults, likely because parental adults brought their chicks to bayside foraging areas. Piping plovers are highly territorial (Elliot-Smith and Haig 2004), so if parental adults were including bayside foraging habitats in territorial boundaries, they may have forced non-parental adults, particularly those whose broods were not on the bayside, to forage elsewhere. Further, post-breeding birds were observed at similar distances to bay intertidal habitat as birds exhibiting parental behaviors, suggesting that this possible territorial avoidance was released once an individual's chicks fledged. Despite this apparent difference, the effect size of selection for bayside intertidal habitat was small relative to other habitat variables. Therefore, other features of the landscape, such as vegetation, drove adult habitat selection more than bayside habitat.

There was more suitable habitat on Fire Island and Westhampton Island for parental plovers than non-parental plovers. Fire Island is not a known migration hot spot for plovers or other shorebird species. While the island does support some north and southward migrants from other breeding areas, such as Atlantic Canada, there are far more important stopover areas in the Atlantic plover range during migration (Weithman et al. 2018). Instead, in the years of this study, Fire Island was a highly productive breeding site with high reproductive output and immigration of breeding birds (Robinson et al. 2020*b*) as the breeding population exponentially increased following Hurricane Sandy (Walker et al. 2019, Weithman et al. 2019). To increase habitat suitability for non-parental birds, managers should enhance protection of habitats that non-parental plovers selected, primarily oceanside foraging habitats, which were impacted by vehicular and pedestrian traffic during much of the breeding season (Walker et al. 2019).

Using the predicted habitat suitability maps for piping plovers on Fire Island and Westhampton Island, we can begin to target areas that could serve as future habitat restoration sites. To identify target areas, both suitable and

unsuitable maps illustrating the range of suitability should be used (Boyce et al. 2002). Using only a binary suitability threshold map may discount potentially suitable habitat that predicts close to the boundaries used here, which is illustrated by less than 75% of our used points falling into the suitable habitat category. Therefore, multiple methods of evaluating habitat suitability improve on a single threshold (Hernandez et al. 2006). As vegetation proportion was the most influential predictor of habitat selection, it is important to focus future plover habitat management plans on reducing dense vegetation cover, particularly within large parcels of dry sand. Vegetation cover is easily modified due to widespread availability of both mechanical and chemical vegetation removal options (Powell and Collier 2000, Cohen 2005). Bayside intertidal habitat, which also is important to parental plovers, has been achieved through sand placement and should be evaluated as an option for habitat creation for plovers. However, bayside intertidal habitat is a challenging feature to achieve and maintain without significantly altering landscape geomorphology or using annual vegetation management. Alternatively, allowing storms like Hurricane Sandy to alter the island naturally can increase the overall amount of bayside intertidal habitat for plovers (Cohen et al. 2009, Walker et al. 2019). Prior to Hurricane Sandy, unvegetated bay intertidal was limited in our study area, and plovers nested primarily on oceanfront beaches. Following Hurricane Sandy, overwash areas were among the most suitable areas for adult plovers, demonstrating plasticity in nesting habitat selection. Furthermore, plovers were still selecting for Hurricane-created habitat six years after the storm, illustrating the long-term benefits of natural processes. The protection of intertidal habitats also benefits other migratory shorebirds, such as the federally threatened *rufa* red knot (*Calidris canutus rufa*, Monk et al. 2020), and may be increasingly necessary for other shorebird species with the accelerating loss of intertidal wetlands and climate change (Iwamura et al. 2013, Davidson 2014).

Nest-site selection studies generally are congruent with the habitat selection of parental adults in this study, but, in some cases, disagree with non-parental adult selection. Further, we did not consider microhabitat selection, such as substrate type or nest-site composition, so we cannot make comparisons between habitat selection of adults and nests at very fine scales. Similar to what has been found for nest-site selection, adults of both behavioral classes were selecting for areas at lower elevation (relative to dunes; Maslo et al. 2011). In this study, we evaluated the suitability of intertidal areas that were unavailable for nesting. These intertidal areas were the most suitable to non-parental plovers, demonstrating the divide between nest-site selection and adult habitat selection. Other plovers display similar selection patterns to piping plovers; for example, snowy plovers (*Charadrius nivosus*) select for wide beaches that are less sloped (Leja 2015). Kentish plovers (*Charadrius alexandrinus*) select nest sites with higher visibility, which was hypothesized to improve the ability to detect predators and avoided human disturbance (Gómez-Serrano and López-López 2014, Fraser and Catlin 2019).

As methodologies improve for more detailed monitoring of wildlife taxa, the opportunities to monitor and assess differences in habitat associations among and within life cycle stages will also improve. Here, we illustrated that dividing a single portion of the life cycle can result in different associations with landscape features. As habitat selection of adults also does not entirely align with nest-site selection, habitat evaluation should not just consider the placement of nests, but also must consider habitat needs of other plover life stages. This need for a broader focus of habitat management is similar to what was suggested for the Great Plains piping plover population; focusing solely on nesting habitat can be detrimental to piping plover chicks by creating an ecological trap (Wiltermuth et al. 2015). We propose that the same is true for adult piping plover management on the Atlantic Coast. Continuing to study the various life stages of plovers can lend insight into whether behavioral habitat selection differs among populations or within smaller geographic areas. Future work on this issue could focus on chick habitat selection in this novel post-storm landscape to see whether further differences exist between pre-fledged broods and adults and whether selection relationships track survival relationships or species persistence. These differences also may be greater across different portions of the life cycle, such as for migratory species, and thus, future

work should also evaluate differences in habitat use and selection among life cycle stages.

Acknowledgments

This project was funded by money provided by the U.S. Army Corps of Engineers to the U.S. Fish and Wildlife Service under the Fire Island to Moriches Inlet Biological Opinion and by Virginia Tech. We thank R. Smith and P. Weppler, U.S. Army Corps of Engineers and S. Papa, U.S. Fish and Wildlife Service for supporting this work. We also thank the Virginia Tech Open Access Subvention Fund for support of this work. We thank A. McIntyre and T. Byrne from New York State Parks, L. Ries and M. Bilecki from the National Park Service, N. Gibbons and D. Sanford from Suffolk County Parks, and K. Jennings and F. Hamilton from New York State Department of Environmental Conservation for permission to work on their property and various kinds of support. We thank all the Fire Island technicians and crew leaders that tirelessly collected the field data used in this study. We thank S. Prisley, C. Weithman, and two anonymous reviews for reviewing and helping greatly to improve an earlier version of this manuscript. We acknowledge the Tutelo/Monacan people, who are the traditional custodians of the land upon which Virginia Tech now sits. Likewise, we acknowledge the Shinnecock, Mauntaukett, and Unkechaug peoples, the traditional custodians of the land where fieldwork was conducted. We recognize the continuing connection of these peoples to the land, water, and air of these places. We pay respect to their elders past, present, and emerging. This research was conducted under Virginia Tech Institutional Animal Care and Use Committee protocols #14-003 and #16-244, U.S. Geological Survey Federal Bird Banding permit #21446, U.S. Fish and Wildlife Service Endangered Species permit #TE-697823, U.S. National Park Service Scientific Research and Collecting permits FIIS-2016-SCI-0003, FIIS-2017-SCI-0004, FIIS-2018-SCI-0004, New York State Department of Environmental Conservation Endangered Species permit #314, New York State Office of Parks, Recreation and Historic Preservation permits 16-0393, 17-0755, 18-0168 and permits for Research in Suffolk County Parklands.

Literature Cited

Ahlering, M. A., and J. Faaborg. 2006. Avian habitat management meets conspecific attraction: If you build it, will they come? The Auk 123:301–312.

Anteau, M. J., T. L. Shaffer, M. T. Wiltermuth, and M. H. Sherfy. 2014. Landscape selection by Piping Plovers has implications for measuring habitat and population size. Landscape Ecology 29:1033–1044.

Bellman, H. A. 2018. Hurricane and human-induced habitat changes on Fire Island and Westhampton Island, New York, and the effects on breeding Piping Plovers (*Charadrius melodus*). Thesis. Virginia Tech, Blacksburg, Virginia, USA.

Black, K. M. 2021. Red fox ecology and interactions with piping plovers on Fire Island, New York. Dissertation. Virginia Tech, Blacksburg, Virginia, USA.

Bloom, P. M., R. G. Clark, D. W. Howerter, and L. M. Armstrong. 2013. Multi-scale habitat selection affects offspring survival in a precocial species. Oecologia 173:1249–1259.

Boulinier, T., and E. Danchin. 1997. The use of conspecific reproductive success for breeding patch selection in terrestrial migratory species. Evolutionary Ecology 11:505–517.

Boyce, M. S. 2006. Scale for resource selection functions. Diversity and Distributions 12:269–276.

Boyce, M. S., P. R. Vernier, S. E. Nielsen, and F. K. Schmiegelow. 2002. Evaluating resource selection functions. Ecological Modelling 157:281–300.

Boyne, A. W., D. L. Amirault-Langlais, and A. J. McCue. 2014. Characteristics of Piping Plover nesting habitat in the Canadian Maritime Provinces. Northeastern Naturalist 21:164–173.

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. 1987. Physical and social determinants of nest-site selection in Piping Plover in New Jersey. Condor 89:811–818.

Burger, J. 1994. The effect of human disturbance on foraging behavior and habitat use in Piping Plover (*Charadrius melodus*). Estuaries 17:695–701.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference. Second edition. Springer, New York, New York, USA.

Cairns, W. E. 1982. Biology and behavior of breeding Piping Plovers. Wilson Bulletin 94:531–545.

Caughley, G. 1994. Directions in conservation biology. Journal of Animal Ecology 63:215–244.

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.

Cohen, J. B. 2005. Factors limiting Piping Plover nesting pair density and reproductive output on Long Island, New York. Dissertation. Virginia Tech, Blacksburg, Virginia, USA.

Cohen, J. B., and J. D. Fraser. 2010. Piping plover foraging distribution and prey abundance in the pre-

laying period. Wilson Journal of Ornithology 122:578–582.

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.

Cohen, J. B., S. M. Karpanty, D. H. Catlin, J. D. Fraser, and R. A. Fischer. 2008*a*. Winter ecology of Piping Plovers at Oregon Inlet, North Carolina. Waterbirds 31:472–479.

Cohen, J. B., E. H. Wunker, and J. D. Fraser. 2008*b*. Substrate and vegetation selection by nesting Piping Plovers. Wilson Journal of Ornithology 120:404–407.

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.

Davidson, N. C. 2014. How much wetland has the world lost? Long-term and recent trends in global wetland area. Marine and Freshwater Research 65:934–941.

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.

Dietz, M. S., R. T. Belote, G. H. Aplet, and J. L. Aycrigg. 2015. The world's largest wilderness protection network after 50 years: an assessment of ecological system representation in the U.S. National Wilderness Preservation System. Biological Conservation 184:431–438.

Doligez, B., E. Danchin, and J. Clobert. 2002. Public information and breeding habitat selection in a wild bird population. Science 297:1168–1170.

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.

Elliot-Smith, E., and S. Haig. 2004. Piping Plover (*Charadrius melodus*), version 2.0. *in* A. F. Poole, editor. The birds of North America. Cornell Lab of Ornithology, Ithaca, New York, USA.

Flemming, S. P. 1987. Natural and experimental adoption of Piping Plover chicks (*Charadrius melodus*). Journal of Field Ornithology 58:270–273.

Flemming, S. P., R. D. Chiasson, and P. J. Austin-Smith. 1992. Piping Plover nest site selection in New Brunswick and Nova Scotia. Journal of Wildlife Management 56:578–583.

Fraser, J. D., and D. H. Catlin. 2019. Habitat ecology and conservation of Charadrius plovers. Pages 217–243 *in* M. A. Colwell, and S. M. Haig, editors. The population ecology and conservation of Charadrius plovers (no. 52). CRC Press, Boca Raton, Florida, USA.

Fraser, J. D., S. E. Keane, P. A. Buckley, J. D. Fraser, S. E. Keane, and P. A. Buckley. 2005. Prenesting use of intertidal habitats by Piping Plovers on South Monomoy Island, Massachusetts. Journal of Wildlife Management 69:1731–1736.

Gibson, D., et al. 2018. Impacts of anthropogenic disturbance on body condition, survival, and site fidelity of nonbreeding Piping Plovers. The Condor: Ornithological Applications 120:566–580.

Gómez-Serrano, M. A., and P. López-López. 2014. Nest site selection by kentish plover suggests a trade-off between nest-crypsis and predator detection strategies. PLoS One 9:e107121.

Haig, S. M., and L. Oring. 1985. Distribution and status of the piping plover throughout the annual cycle. Journal of Field Ornithology 56:334–345.

Haig, S. M., and L. W. Oring. 1988. Mate, site, and territory fidelity in Piping Plovers. The Auk 105:268–277.

Hapke, C., O. Brenner, R. Hehre, and B. Reynolds. 2013. Coastal change from Hurricane Sandy and the 2012–13 winter storm season: fire Island, New York. Page U.S. Geological Survey Open-File Report 2013-1231.

Hernandez, P. A., C. H. Graham, L. L. Master, and D. L. Albert. 2006. The effect of sample size and species characteristics on performance of different species distribution modeling methods. Ecography 29:773–785.

Hijmans, R. J. 2016. Raster: geographic data analysis and modeling. R package version 2.5-8. https://CRAN.R-project.org/package=raster

Hostetler, J. A., T. S. Sillett, and P. P. Marra. 2015. Full-annual-cycle population models for migratory birds. The Auk 132:433–449.

Huggett, A. J. 2005. The concept and utility of "ecological thresholds" in biodiversity conservation. Biological Conservation 124:301–310.

Hunt, K. L., J. D. Fraser, M. J. Friedrich, S. M. Karpanty, and D. H. Catlin. 2018. Demographic response of an imperiled bird suggests that engineered habitat restoration is no match for natural riverine processes. Condor 120:149–165.

Iwamura, T., H. P. Possingham, I. Chadès, C. Minton, N. J. Murray, D. I. Rogers, E. A. Treml, and R. A. Fuller. 2013. Migratory connectivity magnifies the consequences of habitat loss from sea-level rise for shorebird populations. Proceedings of the Royal Society B: Biological Sciences 280:20130325.

Jaramillo, E., A. McLachlan, and P. Coetzee. 1993. Intertidal zonation patterns of macroinfauna over a

range of exposed sandy beaches in south central Chile. Marine Ecology Progress Series 101:105–118.

Jiménez-Valverde, A., P. Acevedo, A. M. Barbosa, J. M. Lobo, and R. Real. 2013. Discrimination capacity in species distribution models depends on the representativeness of the environmental domain. Global Ecology and Biogeography 22:508–516.

Jones, J. 2001. Habitat selection studies in avian ecology: a critical review. The Auk 118:557–562.

Le Fer, D., J. D. Fraser, and C. D. Kruse. 2008. Piping Plover foraging-site selection on the Missouri River. Waterbirds 31:587–592.

Leatherman, S. P. 1988. Barrier Island handbook. The University of Maryland, College Park, Maryland, USA.

Leja, S. 2015. Habitat selection and response to restoration by breeding western snowy plovers in coastal northern California. Thesis. Humboldt State University, Arcata, California, USA.

Lima, S. L., and P. A. Zollner. 1996. Towards a behavioral ecology of ecological landscapes. Trends in Ecology and Evolution 11:131–135.

Lindström, Å., and T. Piersma. 1993. Mass changes in migrating birds: the evidence for fat and protein storage re-examined. Ibis 135:70–78.

Loegering, 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.

Marra, P. P., E. B. Cohen, S. R. Loss, J. E. Rutter, and C. M. Tonra. 2015. A call for full annual cycle research in animal ecology. Biology Letters 11: 20150552.

Maslo, B., S. N. Handel, and T. Pover. 2011. Restoring beaches for Atlantic coast Piping Plovers (*Charadrius melodus*): a classification and regression tree analysis of nest-site selection. Restoration Ecology 19:194–203.

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., S. L. Zeigler, E. C. Drake, T. Pover, and N. G. Plant. 2019. A pragmatic approach for comparing species distribution models to increasing confidence in managing Piping Plover habitat. Conservation Science and Practice 2:e150.

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.

McGowan, C. P., D. H. Catlan, G. D. Jons, and G. A. Pavelka. 2007. Piping Plovers nesting amongst cottonwood saplings. Waterbirds 30:275–277.

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.

Moermond, T. C. 1979. Habitat constraints on the behavior, morphology, and community structure of anolis lizards. Ecology 60:152–164.

Monk, J. D., E. Kwon, A. DeRose-Wilson, S. G. Robinson, H. A. Bellman, S. M. Karpanty, D. H. Catlin, and J. D. Fraser. 2020. Extensive use of intertidal habitat by shorebirds outside protected nesting areas. Journal of Wildlife Management 84:1338–1347.

Morris, L. R., K. M. Proffitt, and J. K. Blackburn. 2016. Mapping resource selection functions in wildlife studies: concerns and recommendations. Applied Geography 76:173–183.

National Oceanic and Atmospheric Administration [NOAA]. 2017. National Centers for Environmental Information. Daily temperature and precipitation for Westhampton, New York. https://www.ncdc.noaa.gov/cdo-web/results

Paasivaara, A., and H. Pöysä. 2008. Habitat-patch occupancy in the common goldeneye (*Bucephala clangula*) at different stages of the breeding cycle: implications to ecological processes in patchy environments. Canadian Journal of Zoology 86:744–755.

Paterson, J. E., B. D. Steinberg, and J. D. Litzgus. 2012. Revealing a cryptic life-history stage: differences in habitat selection and survivorship between hatchlings of two turtle species at risk (*Glyptemys insculpta* and *Emydoidea blandingii*). Wildlife Research 39:408–418.

Powell, A. N., and C. L. Collier. 2000. Habitat use and reproductive success of western snowy plovers at new nesting areas. Journal of Wildlife Management 64:24–33.

R Core Team. 2018. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/

Ray, G. C., and W. P. Gregg. 1991. Establishing biosphere reserves for coastal barrier ecosystems. BioScience 41:301–309.

Robin, X., N. Turck, A. Hainard, N. Tiberti, F. Lisacek, J. C. Sanchez, and M. Müller. 2011. pROC: an open-source package for R and S+ to analyze and compare ROC curves. BMC Bioinformatics 12:77.

Robinson, S. G., J. Fraser, D. Catlin, S. M. Karpanty, J. Altman, R. Boettcher, K. Holcomb, C. Huber, K. Hunt, and A. Wilke. 2019. Irruptions: evidence for breeding season habitat limitation in Piping Plover (*Charadrius melodus*). 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. 2020*b*. Piping Plover population change in a hurricane-affected population and the relation to constructed nesting habitat. The Condor: Ornithological Applications 122. https://doi.org/10.1093/condor/duaa041

Robinson, S. G., C. E. Weithman, H. A. Bellman, S. P. Prisley, J. D. Fraser, D. H. Catlin, and S. M. Karpanty. 2020*a*. Assessing error in locations of conspicuous wildlife using handheld GPS units and location offset methods. Wildlife Society Bulletin 44:163–172.

Roche, E. A., C. M. Dovichin, and T. W. Arnold. 2014. Field-readable alphanumeric flags are valuable markers for shorebirds: use of double-marking to identify cases of misidentification. Journal of Field Ornithology 85:329–338.

Schneider, E. G., and S. R. McWilliams. 2007. Using nest temperature to estimate nest attendance of Piping Plovers. Journal of Wildlife Management 71:1998–2006.

Stantial, M. 2020. Factors limiting abundance and productivity of piping plovers (*Charadrius melodus*) in New Jersey. Dissertation. SUNY College of Environmental Science and Forestry, Syracuse, New York, USA.

Timm, B. C., K. McGarigal, S. A. Cushman, and J. L. Ganey. 2016. Multi-scale Mexican spotted owl (*Strix occidentalis lucida*) nest/roost habitat selection in Arizona and a comparison with single-scale modeling results. Landscape Ecology 31:1209–1225.

Troscianko, J., J. Wilson-Aggarwal, M. Stevens, and C. N. Spottiswoode. 2016. Camouflage predicts survival in ground-nesting birds. Scientific Reports 6:19966.

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.

Walker, S. J., and T. A. Schlacher. 2011. Impact of a pulse human disturbance experiment on macrofaunal assemblages on an Australian sandy beach. Journal of Coastal Research 275:184–192.

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. The Condor: Ornithological Applications 121:duz037.

Westerskov, K. 1950. Methods for determining the age of game bird eggs. Journal of Wildlife Management 14:56–67.

Wilcox, L. R. 1959. A twenty year banding study of the Piping Plover. The Auk 76:129–152.

Wiltermuth, M. T., M. J. Anteau, M. H. Sherfy, and A. T. Pearse. 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.

Data Availability

Geospatial data are sensitive and cannot be provided publicly. Data used in modeling are available from the Virginia Tech Data Repository: https://doi.org/10.7294/16796320.

Supporting Information

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.3870/full