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RESEARCH ARTICLE

Impacts of anthropogenic disturbance on body condition, survival, and site fidelity of nonbreeding Piping Plovers

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ABSTRACT

The impact of habitat loss on shorebirds may be exacerbated by disturbance from human recreational use, which further reduces the amount of coastal habitat that is functionally available. This can have consequences for the condition of individual birds or for population processes, both of which should be considered in strategies to reduce conflict between shorebirds and recreational users of coastal habitat. Our objectives were to determine the associations between human recreational use, coastal habitat modifications, and Piping Plover (*Charadrius melodus*) body condition and demography. We monitored banded Piping Plovers throughout their annual cycle to assess variation in body condition, true survival, and site fidelity related to disturbance regimes in 8 geographically proximate, nonbreeding areas along the southeastern Atlantic Coast of North America from 2012 to 2016. Piping Plovers in disturbed sites were 7% lighter than those in less disturbed sites. Additionally, true annual survival was lower in more disturbed areas. However, site fidelity was less influenced by disturbance than were body mass and survival. Movements away from specific nonbreeding areas were uncommon, regardless of disturbance regime, but individuals that moved to new wintering locations had high probabilities of annual survival ($\bar{S} = 0.80$) relative to their site-faithful counterparts ($\bar{S} = 0.67$). Associations among nonbreeding conditions, body condition, and demography highlight the importance of nonbreeding habitats to annual population dynamics of migratory species. Conservation strategies for Piping Plovers that focus solely on breeding season dynamics may not account for some of the mechanisms that influence demographic rates and population trajectories.

Keywords: nonbreeding demography, body condition, true survival, anthropogenic disturbance, shorebird conservation, Piping Plover, *Charadrius melodus*

Impactos del disturbio antrópico en la condición corporal, la supervivencia y la fidelidad al sitio de individuos no reproductivos de *Charadrius melodus*

RESUMEN

El impacto de la pérdida de hábitat en las aves playeras puede verse exacerbado por los disturbios producidos por el uso recreativo humano, lo que reduce aún más la cantidad de hábitat costero que está funcionalmente disponible. Esto puede tener consecuencias para la condición de las aves individuales o para los procesos poblacionales, siendo importante considerar ambos en las estrategias para reducir el conflicto entre las aves playeras y los usuarios recreativos del hábitat costero. Nuestros objetivos fueron determinar las asociaciones entre el uso recreativo humano, las modificaciones del hábitat costero y la condición corporal y la demografía de *Charadrius melodus*. Monitoreamos individuos anillados de *C. melodus* a lo largo del ciclo anual para evaluar la variación en la condición corporal, la supervivencia verdadera y la fidelidad al sitio en relación con los regímenes de disturbio en ocho áreas no reproductivas geográficamente cercanas a lo largo del sureste de la costa atlántica de América del Norte desde 2012 a 2016. Los individuos de *C. melodus* en los sitios disturbados fueron 7% más livianos que en sitios menos disturbados. Adicionalmente, la supervivencia anual verdadera fue más baja en las áreas más disturbadas. Sin embargo, la fidelidad al sitio estuvo menos influenciada por el disturbio que la masa corporal y la supervivencia. Los movimientos alejándose de las áreas no reproductivas específicas fueron poco comunes independientemente del régimen de disturbio, pero

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los individuos que se movieron hacia nuevos lugares de invernada tuvieron altas probabilidades de supervivencia anual ($\bar{S} = 0.80$) en comparación con sus contrapartes fieles al sitio ($\bar{S} = 0.67$). Las asociaciones entre condiciones no reproductivas, condición corporal y demografía subrayan la importancia de los hábitats no reproductivos en las dinámicas poblacionales anuales de una especie migratoria. Las estrategias de conservación de *C. melodus* enfocadas solamente en las dinámicas de la estación reproductiva pueden no considerar algunos de los mecanismos que influencian las tasas demográficas y la trayectoria poblacional.

Palabras clave: Charadrius melodus, condición corporal, conservación de aves playeras, demografía no reproductiva, disturbio antrópico, supervivencia verdadera

INTRODUCTION

Loss and degradation of coastal habitats is a major threat to many shorebird species. A review of threats to shorebirds (Kirby et al. 2008) demonstrated that migratory and overwintering habitats continue to be lost or degraded (e.g., reduction of macroinvertebrate prey, destruction of foraging or roosting areas) through shoreline modifications (e.g., beach nourishment, inlet stabilization, sand mining, and wrack removal) and, more recently, by climate change and sea-level rise (Iwamura et al. 2013, Wauchope et al. 2017). Furthermore, the impact of habitat degradation on shorebirds is exacerbated by increased human recreational use (e.g., off-leash dog walking, off-road vehicle use) that reduces the amount of functional coastal habitat available for shorebirds (Foster et al. 2009, Tarr et al. 2010). However, the overall impacts of human recreational use on the population dynamics of shorebirds have been difficult to quantify, and conservation measures aimed at reducing conflict between shorebirds and recreational users of the coast are often controversial or not effective (Melvin et al. 1991, Weston et al. 2012, Schlacher et al. 2013b).

Many human beach-related activities, such as allowing dogs off-leash, are perceived by beachgoers as ecologically benign (Williams et al. 2009), but these types of disturbance have been negatively associated with shorebird behavior and demography (Ruhlen et al. 2003, Foster et al. 2009, Burger and Niles 2013, Schlacher et al. 2013a). However, the mechanisms by which disturbance influences local population dynamics remain unclear. Recreational anthropogenic disturbances have been associated with reductions in the foraging rates of shorebirds (Fitzpatrick and Bouchez 1998, Beale and Monaghan 2004, Yasue 2006), which could impair an individual's ability to acquire the energy reserves necessary for future survival or reproduction (Goss-Custard and Verboven 1993). At the level of individual birds, if the perceived fitness costs associated with anthropogenic disturbances outweigh the perceived costs of finding and occupying less disturbed habitat, emigration may be a mechanism to ameliorate these fitness costs. Unfortunately, from both an observational and analytical viewpoint, emigration and mortality are often confounded (Cormack 1964). From a conservation perspective, however, it is critical to separate emigration from mortality (Marshall et al. 2004).

Piping Plovers (*Charadrius melodus*) are imperiled temperate shorebirds that nest in the northern Atlantic Coast, Great Plains, and Great Lakes regions of North America. Many Piping Plovers from the Great Lakes and Atlantic Coast breeding populations migrate through or winter on the southeastern coast of the United States (Gratto-Trevor et al. 2012, Weithman et al. 2018). Although the numbers of breeding pairs in each population have substantially increased since the species was listed in 1985 (Hecht and Melvin 2009), population growth has slowed recently, despite relatively high reproductive output (e.g., Saunders et al. 2014). The reductions in population growth have been driven by density-dependent processes (e.g., competition for high-quality nesting or brood-rearing habitats; Cohen et al. 2009) on the breeding grounds, but habitat conditions on the migratory or wintering grounds may also influence the numbers of individuals that return to the breeding grounds (Roche et al. 2010). Even if Piping Plover populations are regulated primarily by conditions on the breeding grounds, poor conditions at nonbreeding locations could result in increased demographic stochasticity on the breeding grounds, thereby increasing local extinction risk, especially for small populations (Halley and Iwasa 1998). Although shorebird populations can be influenced by conditions in their wintering, migratory, and breeding habitats, the influence of nonbreeding habitat conditions on population dynamics remains understudied (Fernández and Lank 2008).

The goals of this study were to: (1) evaluate the impacts of anthropogenic disturbance along the southeastern Atlantic Coast nonbreeding grounds on Piping Plover body condition; and (2) identify whether individuals in more disturbed overwintering habitats had increased mortality or emigration rates. Here, we define anthropogenic disturbance very broadly as consisting of both recreational and engineering disturbances. Recreational disturbance includes the general use of coastlines for human recreational activities, which tend to be frequent, although each individual action may result in only a minor coastal disturbance. Engineering disturbances include large-scale restructuring of coastlines (e.g., beach renourishment, channel modifications) or the surrounding area (e.g., development), which, while less frequent, may have a substantial or long-term impact on local ecosystem function. We hypothesized that Piping Plover body

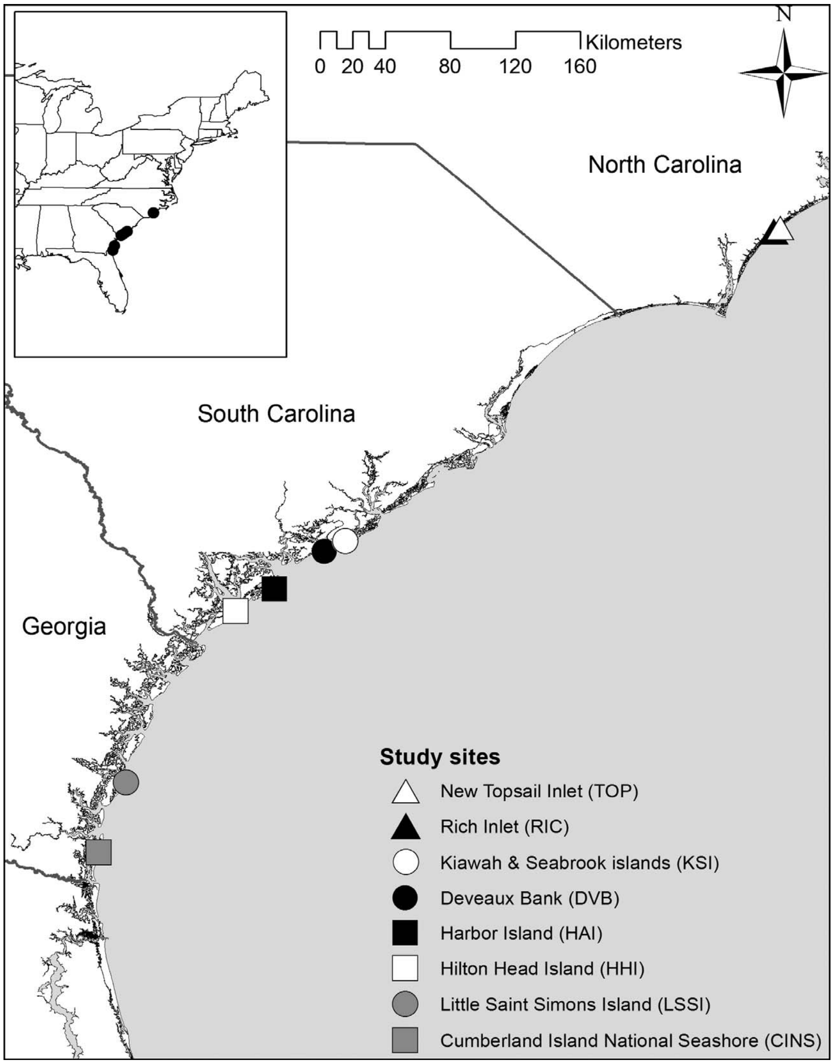

FIGURE 1. Map of our study sites located in North Carolina (New Topsail Inlet and Rich Inlet), South Carolina (Kiawah and Seabrook islands, Deveaux Bank, Harbor Island, and Hilton Head Island), and Georgia (Little Saint Simons Island and Cumberland Island National Seashore), USA, where we examined associations between human recreational use, coastal habitat modifications, and Piping Plover body condition and demography from 2012 to 2016. The inset map depicts our monitored study areas within the eastern United States.

condition would be negatively associated with anthropogenic disturbance, resulting in both reduced annual survival and reduced site fidelity. Thus, we developed a demographic model that incorporated observations of marked individuals within our study area and out-of-area observations of individuals throughout the species' breeding and nonbreeding ranges to simultaneously estimate true survival and fidelity.

METHODS

Field Methods

Study sites. We monitored 4 study regions used by Piping Plovers as stopover and overwintering habitat in North Carolina, South Carolina, and Georgia (Figure 1). Each study region comprised 2 sites that were geographically proximate (within 30 km of each other) and, in general, experienced similar weather conditions. Based on surveys conducted via the 5-yr international Piping Plover census, each study region usually hosted >25% of the state's overwintering Piping Plover population (Elliott-Smith et al. 2009, 2015).

In the North Carolina study region, we surveyed plover habitat near Rich Inlet and New Topsail Inlet, both near Wilmington, from 2010 to 2016. Rich Inlet has not received major shoreline alterations and its main channel is not maintained. It receives moderate levels of recreational use. New Topsail Inlet is a designated shallow-draft inlet and receives regular (∼annual) dredging that follows the deepest existing channel. It receives moderate levels of recreational use from boaters and beachgoers.

In the South Carolina study region, we monitored Kiawah and Seabrook islands and Deveaux Bank, collectively the South Carolina–North study unit, and Harbor Island and Hilton Head Island, collectively the South Carolina–South study unit, from 2012 to 2017. These areas consist of both developed and undeveloped beaches. Kiawah and Seabrook islands have developed coastlines separated by an inlet that has been relocated by cutting a new channel and closing the existing channel with a sand dike. The islands experience high levels of human recreational use. Deveaux Bank is a bird sanctuary protected by the South Carolina Department of Natural Resources, with restricted public access. Harbor Island is a relatively low-disturbance private barrier island but with residential development. Experimental plastic seawalls, sandbags, and sand scraping have been used as emergency measures to protect personal property, but no beach renourishment or stabilization projects have been undertaken. Hilton Head Island has residential development. It has also been modified with a terminal groin, which runs adjacent to an inlet near the center of the island, and the beach has been renourished several times. The island experiences high levels of human recreational use.

In the Georgia study region, we monitored the Little Saint Simons Island complex and Cumberland Island National Seashore in 2010–2017. There were no efforts to renourish or stabilize beaches at either of these 2 sites in Georgia, and human activity was low and carefully managed. Little Saint Simons Island is a privately owned island accessed by a limited number of guests. This study site also included 1 state and 1 federally protected island with no public access. Cumberland Island National Seashore is accessible only by boat and the number of visitors is restricted. It has few access points along its ∼30-km beachfront, leaving much of the beach undisturbed by foot traffic.

Three of our study regions (North Carolina, South Carolina–North, and South Carolina–South) contained both a low- and a high-disturbance site, whereas our final study region (Georgia) consisted of 2 sites with relatively low levels of human activity and development (Figure 2). Because of similarly low disturbance levels, we used the 2 Georgia sites to assess whether geographically similar sites experiencing similar disturbance regimes would exhibit similar demographic patterns.

Capture and handling. Most Piping Plover banding has occurred throughout the species' breeding range (e.g., Catlin et al. 2015, Saunders et al. 2014), which resulted in banded birds occupying our nonbreeding study area. Here, we define the nonbreeding period as the period during an individual's lifecycle that it is either migrating, at a stopover site, or overwintering, as it is likely that each of our monitored sites served birds in each category. Additionally, we captured, weighed (to within 0.1 g), aged (hatch-year [HY] or after-hatch-year [AHY], and second-year [SY] or after-second-year [ASY], depending on the month of capture; Gratto-Trevor 2011), and banded Piping Plovers at our study sites in South Carolina and Georgia to evaluate differences in body condition among individuals associated with different levels of disturbance. We used drop-nets and whoosh-nets to capture foraging and roosting plovers (Sutherland et al. 2004, Doherty 2009). Upon capture, we marked each individual with a metal U.S. Geological Survey (USGS) band and either a green, field-readable, alphanumeric-coded leg flag or a unique combination of 4 color bands and a green Darvic flag.

Monitoring. To understand the demography of Piping Plovers within and among disturbance regimes at overwintering sites along the Atlantic Coast, we surveyed foraging and roosting habitats in each study site. Observers visited each site once every ∼1–4 weeks during the nonbreeding period (September–April) and surveyed all potential habitat. Each survey consisted of researchers: (1) counting all observed Piping Plovers and designating each as banded, unbanded, or unknown band status, and (2) recording the unique band combinations of all banded birds observed. We also counted potential anthropogenic disturbances (i.e. pedestrians, vehicles, and dogs) during each survey. These counts of disturbances were used to develop a disturbance index, which was applied in demographic models as a covariate representing spatial variation in disturbance.

Ancillary resightings. We collected observations of banded individuals that were seen in our study areas from 2012 to 2016 that also were observed elsewhere to separate apparent survival into its constituent demographic processes (i.e. true survival [*S*] and site fidelity [*F*]). Our dataset was enhanced by ongoing research projects and monitoring efforts throughout all 3 breeding locations, along migratory routes, and in overwintering habitat along the southeastern Atlantic Coast, Gulf of Mexico, and the Bahamas. In addition to structured survey efforts, Piping Plover band resightings and location data were reported by the public, often including high-resolution photography useful for identification of individual birds. The timing and location of out-of-area observations of individuals that were also observed in our study area were incorporated into our capture histories.

Body condition. Body mass is a good indicator of condition in plovers (Labocha and Hayes 2012, Catlin et al. 2014). We built a regression model that assessed whether body mass was different between disturbed and less disturbed sites to understand the potential mechanisms driving variation in demographic rates. Piping Plovers were only captured on the wintering grounds in

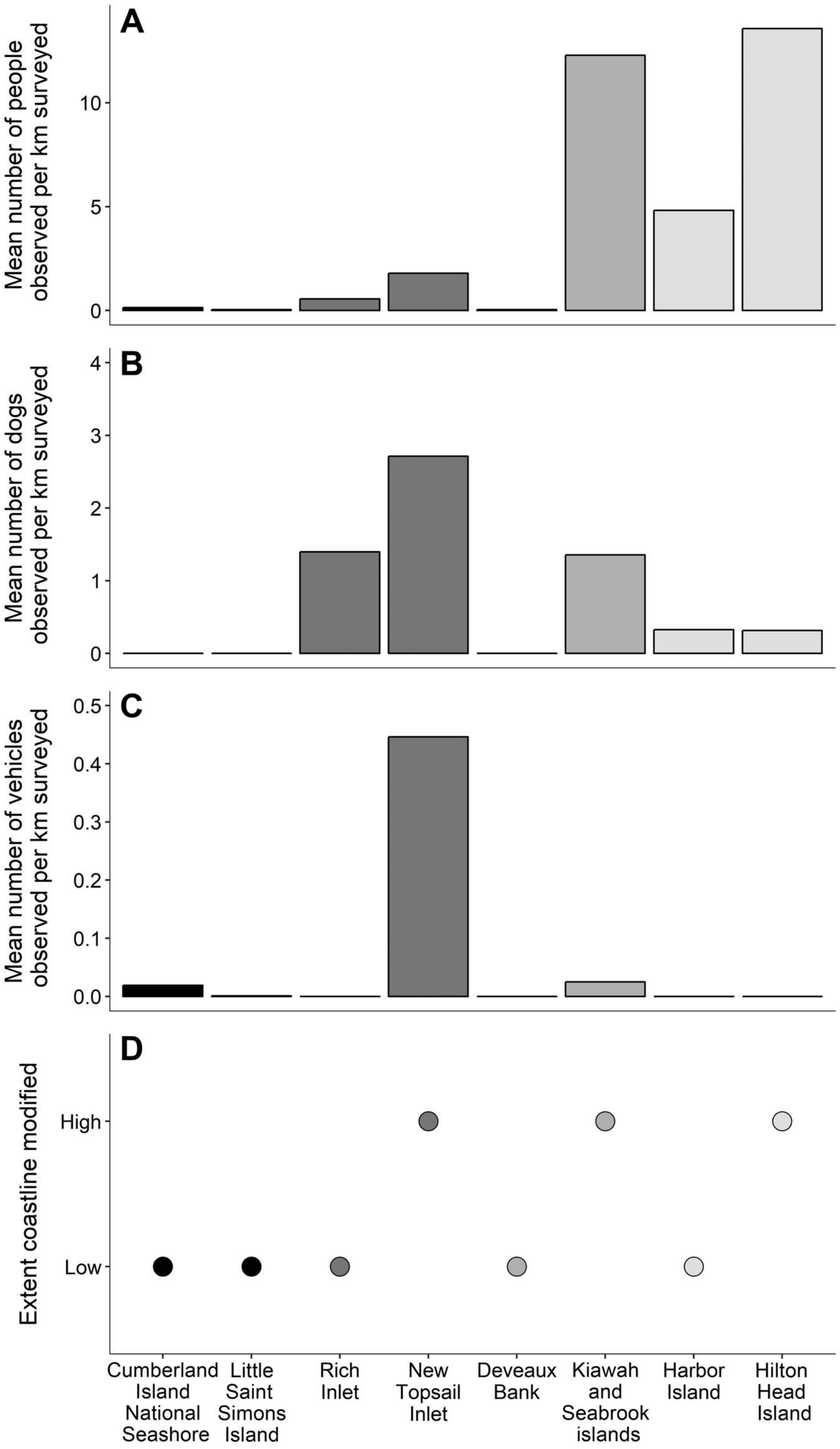

FIGURE 2. Proportion of shorebird surveys during which recreational disturbance was observed: (**A**) mean number of people; (**B**) dogs; and (**C**) terrestrial vehicles (e.g., ATVs, cars, trucks) observed per km; as well as (**D**) the degree to which the coastline was modified throughout each region of our study area. In each of the 4 regions (black = Georgia; dark gray = North Carolina; medium gray = South Carolina–North; light gray = South Carolina–South), there were 2 paired study sites (see Table 1). Coastline modifications included anthropogenic disturbances occurring on the shoreline such as sand renourishment and moving, dredging, and other alterations to a channel.

South Carolina and Georgia. Therefore, this analysis only considered individuals from these sites. We included year ($n = 6$) and month ($n = 6$) of capture, and each individual's age class at capture (HY, AHY, or undetermined), as fixed additive effects in our regression model to account for known sources of temporal and individual variation in body mass. We also included latitude as an individual covariate to account for spatial variation in body size.

Disturbance. Sources of anthropogenic disturbance in our study area (e.g., human, vehicle, and dog recreational use of coastlines) were coarsely measured and potentially correlated ($r > 0.50$) with each other. Therefore, we reduced model complexity by performing a principle component analysis (PCA) on our suite of explanatory disturbance variables, and used the model output as an index of disturbance (hereafter, disturbance index). The PCA analysis included human, vehicle, and dog recreational use indices, calculated as the mean number of people, vehicles, and dogs observed per km surveyed at a given site from 2014 to 2017 (Figure 2), as well as a binomial variable (low or high) that represented the presence or absence of major shoreline modifications (e.g., channel dredging, beach renourishment). We applied the disturbance index in various demographic models (see below) to assess the association between variation in anthropogenic disturbance and Piping Plover demography.

Demographic Models

We developed a novel parameterization of a site-movement multistate model that used (1) observations of individuals within our study area during the nonbreeding season; (2) range-wide observations of individuals during the nonbreeding season; and (3) observations of individuals throughout the breeding range to decouple estimates of true survival (S), site emigration (F), and return immigration (F') from apparent survival (ϕ). The underlying state process model (Figure 3A) consisted of 3 states: (1) alive and within the same study site as during the previous nonbreeding season (hereafter, faithful); (2) alive but not located in the same study site as in the previous nonbreeding season (hereafter, not faithful); and (3) dead:

	$\Psi1_{t+1}$	$\Psi2_{t+1}$	$\Psi3_{t+1}$
$\Psi1_t$	$S''\times F''$	$S''\times(1-F'')$	$1-S''$
$\Psi2_t$	$S'\times F'$	$S'\times(1-F')$	$1-S'$
$\Psi3_t$	0	0	1

The observation process (Figure 3B) was broken into 6 possible outcomes of this state process, in which individuals were either (1) seen (p) in a specific study site during the nonbreeding season and seen during the breeding season; (2) seen in a specific study site during the nonbreeding season but not seen during the breeding season; (3) seen elsewhere during the nonbreeding season and seen during the breeding season; (4) seen elsewhere during the nonbreeding season but not seen during the breeding season; (5) not seen during the nonbreeding season but seen during the breeding season; or (6) not seen during either season. The detection probabilities of the possible observations of the process states during an occasion were defined as follows:

	$\Psi1$	$\Psi2$	$\Psi3$
$p1$	$p^{on}\times p^{breed}$	0	0
$p2$	$p^{on}\times(1-p^{breed})$	0	0
$p3$	0	$p^{off}\times p^{breed}$	0
$p4$	0	$p^{off}\times(1-p^{breed})$	0
$p5$	$(1-p^{on})\times p^{breed}$	$(1-p^{off})\times p^{breed}$	0
$p6$	$(1-p^{on})\times(1-p^{breed})$	$(1-p^{off})\times(1-p^{breed})$	1

Absence from the study area was a partially observable state. This allowed for an identifiable and independent S parameter for individuals that emigrated from the main study area. A critical assumption of this model is that individuals cannot emigrate completely beyond the observable system, or, in other words, individuals must be available for detection at some point during their annual life cycle. Violation of this assumption would bias true survival estimates low, and, depending on the magnitude of the violation, estimates could begin to resemble apparent survival estimates generated from a Cormack-Jolly-Seber model. Under this model parameterization, the on- and off-site detection parameters are partially confounded, which can be alleviated through covariates for either observational process or by incorporating a robust design model for the on-site observation process. Despite this confounding in the observational process, estimation of other parameters remained unbiased (see Supplemental Material Appendix A for a detailed simulation exercise assessing parameter identifiability and bias for this model).

Demographic model development. We were primarily interested in whether anthropogenic disturbance at nonbreeding sites was associated with plover demography. First, we determined the overall amount of spatial variation in demographic rates through a single model that produced site-specific estimates ($n = 8$) for each demographic parameter of interest (S'', F''). Next, we determined the association between disturbance and demographic rate through a model that constrained each demographic rate to be a function of an additive fixed effect of study region ($n = 4$) and our a priori classification of whether a site within a study region was more or less disturbed than the other site within the region, modeled as a fixed-effect categorical variable. We assumed that the proximity of the paired sites meant that geophysical,

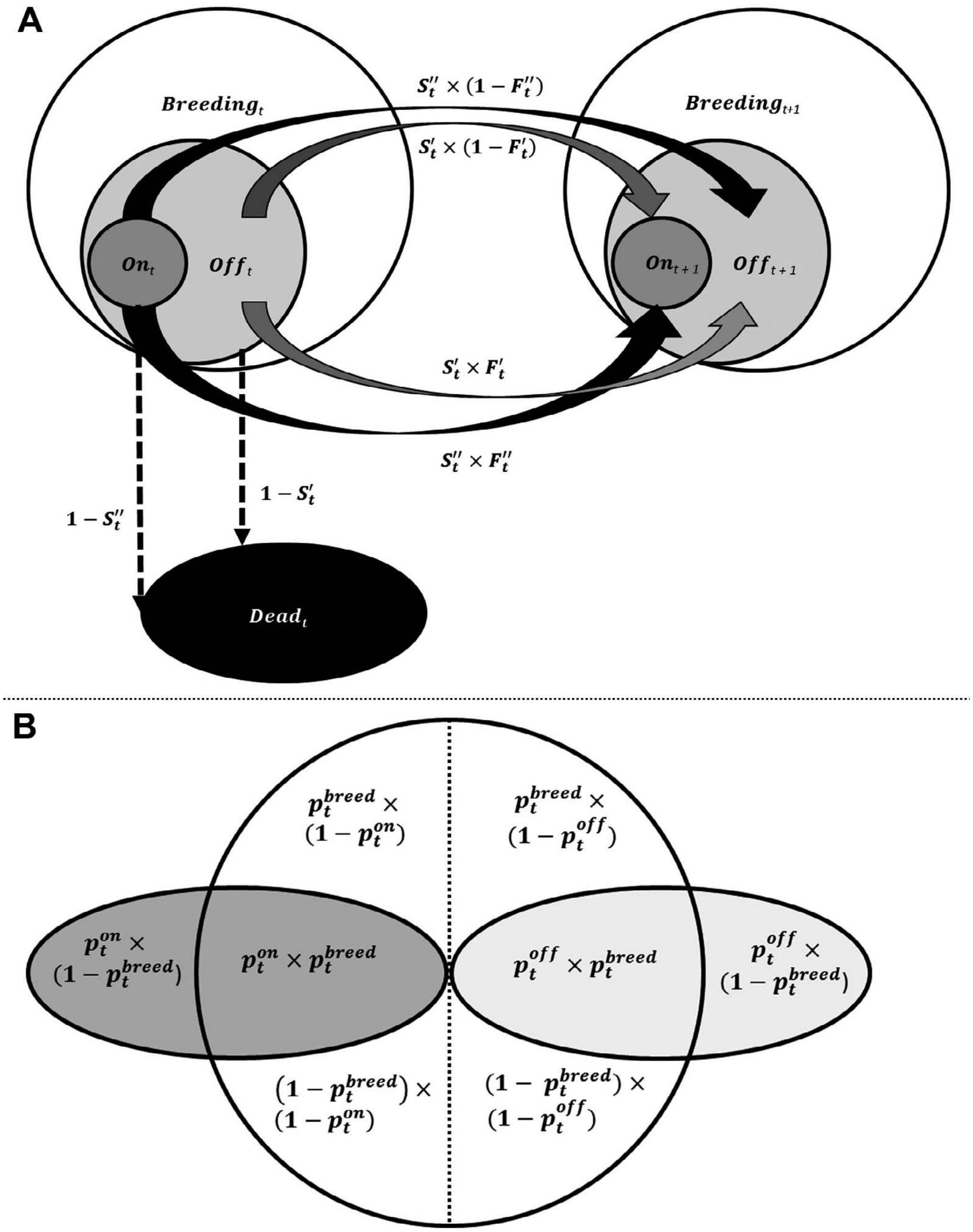

FIGURE 3. Conceptual diagram of the possible (**A**) state transitions, and (**B**) observational process associated with the state process specified in the site-movement model constructed to understand Piping Plover nonbreeding demographic processes. Individuals have the possibility of a unidirectional transition from either the 'On' or the 'Off' state to the 'Dead' state, which represents the probability of permanently leaving the observable population through death (S'': death of nonemigrant adult; S': death of emigrant adult). Individuals also have the possibility of directional transitions between the 'On' and 'Off' states, which represent temporary and permanent emigration (F' and F'') events from our specified study area. The observational process includes the ability to detect individuals within the specified study area, in this case during the nonbreeding season (p^{on}), outside the specified study area, also during the nonbreeding season (p^{off}), and outside the study area but throughout the species' breeding range (p^{breed}).

weather, or other nonhuman-modified environmental processes were similar enough to justify comparison, and therefore that within-pair comparisons would directly assess the overall impact of anthropogenic disturbance on plover demography.

Lastly, we built a model that constrained S'' and F'' to be functions of the observed, continuous index of anthropogenic disturbance. We modeled S'' and F'' to vary as a function of the disturbance index (the first principle component axis from the PCA). Similarly to the previous model, we included study area in this model as a fixed categorical variable to account for potential spatial variation in demography associated with local environmental conditions.

Other variables. Off-site observations of marked individuals were indirectly and variably reported to us through the primary banding organization. Therefore, we constrained both off-site detection parameters (i.e. breeding ground and out-of-area nonbreeding ground resighting rates) to be functions of an additive effect of the primary banding organization (i.e. the Virginia Tech Shorebird Program and direct collaborators [University of Rhode Island and National Audubon Society]; University of Minnesota; Northern Prairie Wildlife Research Center; and other southern Atlantic Coast banders [Environment and Climate Change Canada, and the University of Nebraska]). Birds banded with nonunique field-readable band combinations or banded with only upper leg bands were not included in these analyses as they could not be uniquely identified by sight. We also included breeding population in our model to account for potential differences in survival related to each of our study sites being occupied by different numbers of individuals from each breeding population. Movements among the 3 major breeding populations (i.e. Great Plains, Great Lakes, and Atlantic Coast) are very limited (Catlin et al. 2015). Therefore, we assigned individuals to breeding population based on observations on the breeding grounds, which was possible for 88% of marked individuals. For the remaining 12%, we built a mixture model into the model likelihood that independently assigned individuals of unknown breeding population to either the Atlantic Coast or Great Plains population (the Great Lakes population is ~100% marked) in each model iteration based on the relative proportion of Atlantic Coast to non-Great Lakes Piping Plovers that overwinter in the South Atlantic (0.71; Gratto-Trevor et al. 2012). This mixture parameter allowed all individuals to inform parameter estimation, despite imperfect knowledge of breeding location.

Model specifications. We specified each demographic and body condition model in R (R Core Team 2012) with the package jagsUI (Kellner 2017) to call the Bayesian Gibbs Sampler program JAGS (Plummer 2003). We generated 4 Markov chains, each of 50,000 iterations, with adapt and burn-in phases consisting of an additional 10,000 and 5,000 iterations, respectively, for each analysis, and retained every sample, so that our posterior sample was drawn from 200,000 samples for each parameter. We determined parameter convergence by (1) visually assessing how well the posterior distribution chains were mixed; and (2) using the Brooks-Gelman-Rubin criterion ($\hat{R}$; Brooks and Gelman 1998). We considered models that had $\hat{R} < 1.1$ at each parameter node to have reached convergence.

Model support. Each explanatory model was an assessment of whether anthropogenic disturbance influenced a particular process. Thus, we report beta coefficient (β) values and Bayesian credible intervals (CI) with their beta coefficient posterior probabilities (f). A beta coefficient posterior probability is the proportion of a posterior distribution for each β that has the same sign (positive or negative) as the mean, and represents the probability that the effect size of particular explanatory variable is either greater or less than zero. We considered parameters with at least 95% of the posterior probability greater or less than zero to be indicative of model support.

RESULTS

We performed 1,158 surveys across all of our study sites, resulting in 3,884 observations of 363 uniquely marked Piping Plovers, of which ~80% were originally banded on the breeding grounds. Outside our study area, we received reports of 1,817 resightings of 147 of these individuals between 2010 and 2017. During this period, we captured 94 individuals on the wintering grounds. As survey effort did not become consistent for all 8 study sites until 2012, we only base inference from the demographic model following this point in time.

Disturbance Index

The first axis in the PCA explained 58% of the variation in the disturbance data. Additionally, the first axis had negative loadings for all 4 explanatory variables (Dogs: –0.56; People: –0.28; Vehicles: –0.51; Shoreline modification: –0.58; Supplemental Material Table S1), which indicated that sources of disturbance, in general, covaried with each other, and suggested that the first axis primarily explained variability in disturbance along a continuum of high (–) to low disturbance (+).

Body Condition

After accounting for the effects of latitude, year, seasonality, and age at capture, Piping Plovers captured in more disturbed sites were, on average, 3.74 g (7%) lighter than Piping Plovers captured in less disturbed sites ($\beta = 3.74$, 95% CI: 0.68–6.82, $f = 1.0$; Figure 4).

Demographic Model

On-site detection probabilities during the nonbreeding season were very high across the study area (Figure 5A), ranging from 0.64 to 0.95. Off-site detection probabilities during the nonbreeding season were also high (Figure 5B), but some variation was observed as a function of the primary banding organization. Although detection rates during the breeding season were lower than those during the nonbreeding season, on average, one-third of the individuals observed on the nonbreeding grounds were

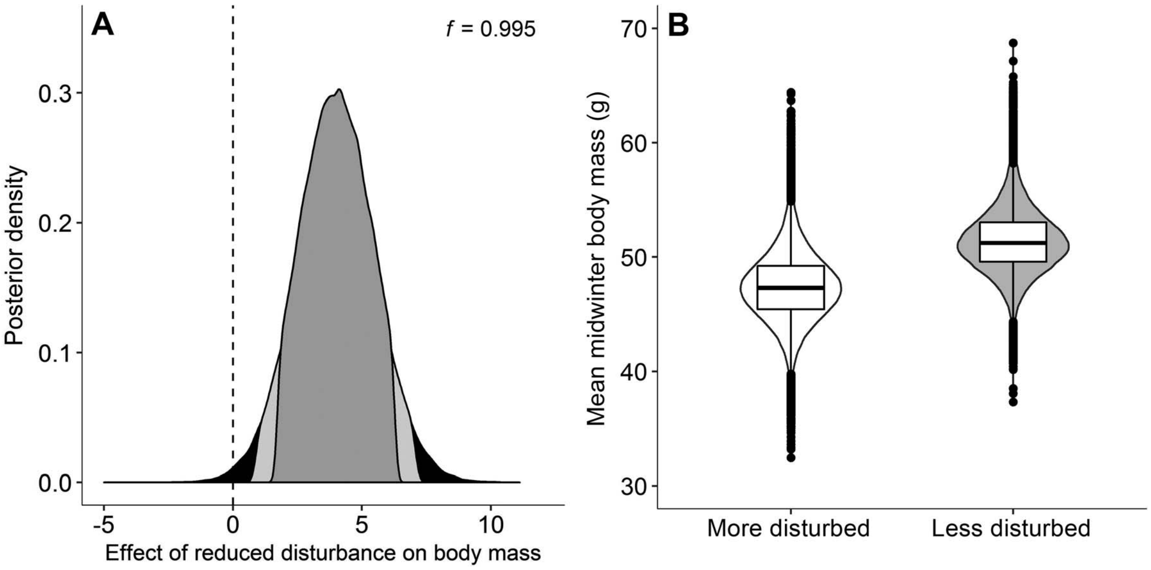

FIGURE 4. (**A**) The posterior density of the disturbance beta coefficient estimate from a linear regression model, which indicated that (**B**) overwintering Piping Plover body mass was ∼3.7 g, or 7% of an average adult overwinting Piping Plover's mass, lower in disturbed sites relative to less disturbed sites. Shading of the posterior density distribution in panel **A** represents the extents of the 50–85% (dark gray), 85–95% (light gray), and 95–100% (black) Bayesian credible intervals. Violin plots in panel **B** represent the observed posterior distribution for overwintering body size at more disturbed (white) and less disturbed (gray) sites, with the median and lower and upper quartiles defined by the box plots. *f* represents the proportion of the posterior density distribution that is greater than zero (dashed vertical line).

also observed by researchers or other interested groups on the breeding grounds (Figure 5C).

Average annual true survival probabilities for site-faithful Piping Plovers (S'') were highly variable among nonbreeding sites (range, S'': 0.50–0.92; Table 1). In agreement with our hypothesis, we found that S'' was, on average, ∼0.10 greater for individuals associated with less disturbed sites than for those in more disturbed sites ($\beta_{disturbance} = 0.48$, 95% CI: –0.08 to 1.04, $f = 0.95$; Figures 6A and 6B). Likewise, we found support for the hypothesis that the continuous disturbance index also influenced S'' ($\beta_{disturbance} = 0.18$, 95% CI: –0.04 to 0.40, $f = 0.95$; Figures 7A and 7B). Despite substantial variation among nonbreeding sites, we found little model support for the hypothesis that an individual's breeding population influenced annual survival (compared with Great Lakes individuals: $\beta_{Atlantic} = -0.13$, 95% CI: –0.62 to 0.37, $f = 0.70$; $\beta_{Plains} = -0.24$, 95% CI: –0.81 to 0.33, $f = 0.80$; Figure 7B). Annual survival rates of nonfaithful individuals (S') were, on average, high relative to those of faithful individuals ($S' = 0.82$, 95% CI: 0.73–0.91), which suggested that emigration from a particular nonbreeding site was not associated with a reduction in survival.

Average site fidelity (F'') also varied among nonbreeding sites, but was generally high (range, F'': 0.73–0.91; Table 1). We found no support for a difference in F'' for individuals associated with less disturbed sites relative to more disturbed sites ($\beta_{disturbance} = 0.41$, 95% CI: –0.56 to 1.37, $f = 0.80$; Figures 6C and 6D); site fidelity was, on average, only 0.04 greater for individuals associated with less disturbed sites. Likewise, we found no support for an association between the continuous disturbance index and F'' ($\beta_{disturbance} = 0.12$, 95% CI: –0.21 to 0.46, $f = 0.75$; Figures 7C and 7D). Following an emigration event, individuals were slightly more likely to remain emigrants (F': 0.59, 95% CI: 0.46–0.71), but returns to original nonbreeding areas were also observed.

DISCUSSION

In this study, we found that Piping Plover body mass was substantially lower for individuals in areas with greater anthropogenic disturbance than for individuals associated with less disturbed habitats. Likewise, survival rates of individuals in disturbed sites were lower than those of plovers in nearby less disturbed sites. Importantly, we found evidence for a greater influence of anthropogenic disturbance on survival than on fidelity, which suggested that individuals associated with disturbed habitats were more likely to leave the population through mortality than by emigration. These results are consistent with the hypothesis that Piping Plovers associated with areas that have greater disturbance experience physiological and

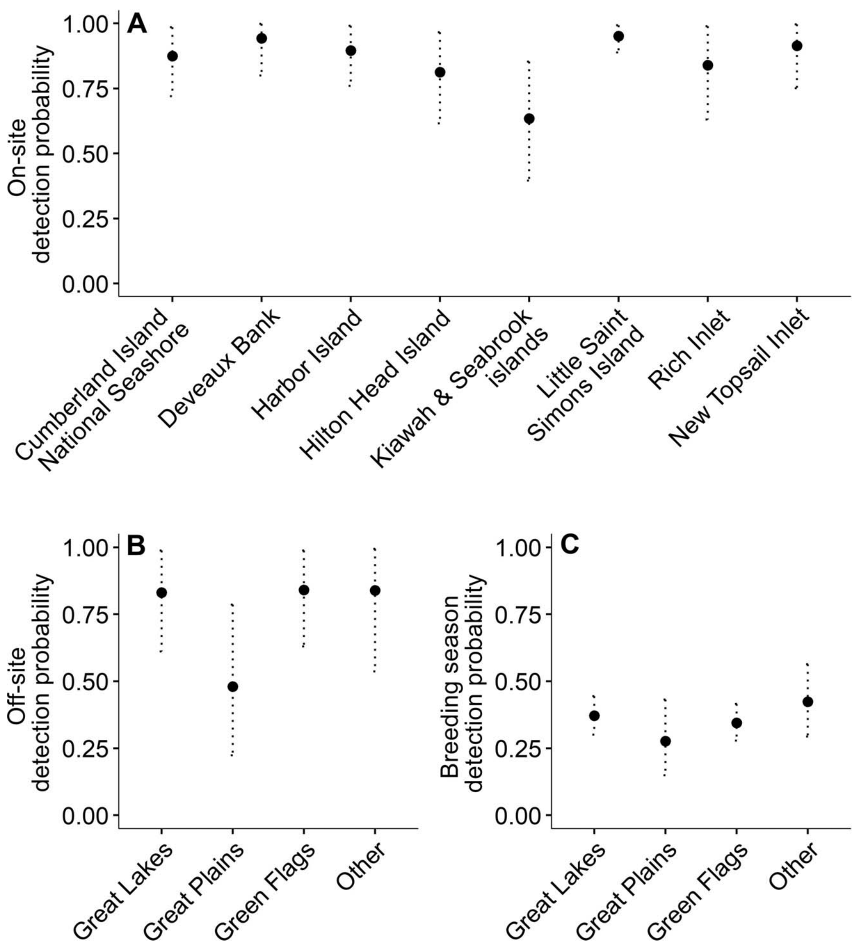

FIGURE 5. (**A**) Average detection probabilities of Piping Plovers during the nonbreeding seasons of 2012–2016 for individuals within the study area were high and relatively spatially constant. (**B**) Off-site detection probabilities during the nonbreeding season varied as a function of the primary banding organization, indicative of variable reporting rates. (**C**) Breeding season detection probabilities were generally constant, regardless of the banding organization. Great Lakes represents birds banded throughout the Great Lakes region by the University of Minnesota; Great Plains represents birds banded by the U.S. Geological Survey; Green Flags represents birds banded by Virginia Tech or the University of Rhode Island throughout the Atlantic Coast or Great Plains regions; and Other represents all other birds marked by another banding group. Error bars represent 95% Bayesian credible intervals.

TABLE 1. Average annual Piping Plover true survival and fidelity rates and associated error (standard deviation) for all study sites located in North Carolina (New Topsail Inlet and Rich Inlet), South Carolina (Kiawah and Seabrook islands, Deveaux Bank, Harbor Island, and Hilton Head Island), and Georgia (Little Saint Simons Island and Cumberland Island National Seashore), along the southeastern U.S. Atlantic Coast, 2012–2016.

Study region	Study site	Disturbance level	Survival ± SD [a]	Fidelity ± SD [a]
North Carolina	New Topsail Inlet	High	0.66 ± 0.08	0.74 ± 0.08
North Carolina	Rich Inlet	Low	0.92 ± 0.08	0.80 ± 0.08
South Carolina–North	Kiawah and Seabrook islands	High	0.55 ± 0.09	0.91 ± 0.06
South Carolina–North	Deveaux Bank	Low	0.50 ± 0.07	0.85 ± 0.07
South Carolina–South	Harbor Island	Low	0.77 ± 0.06	0.91 ± 0.04
South Carolina–South	Hilton Head Island	High	0.62 ± 0.07	0.81 ± 0.07
Georgia	Little Saint Simons Island	Low	0.67 ± 0.04	0.91 ± 0.03
Georgia	Cumberland Island National Seashore	Low	0.68 ± 0.05	0.73 ± 0.06

[a] Estimates were from a model that allowed for independent estimation of the survival and fidelity parameters for each site, and were not constrained by study region or disturbance level.

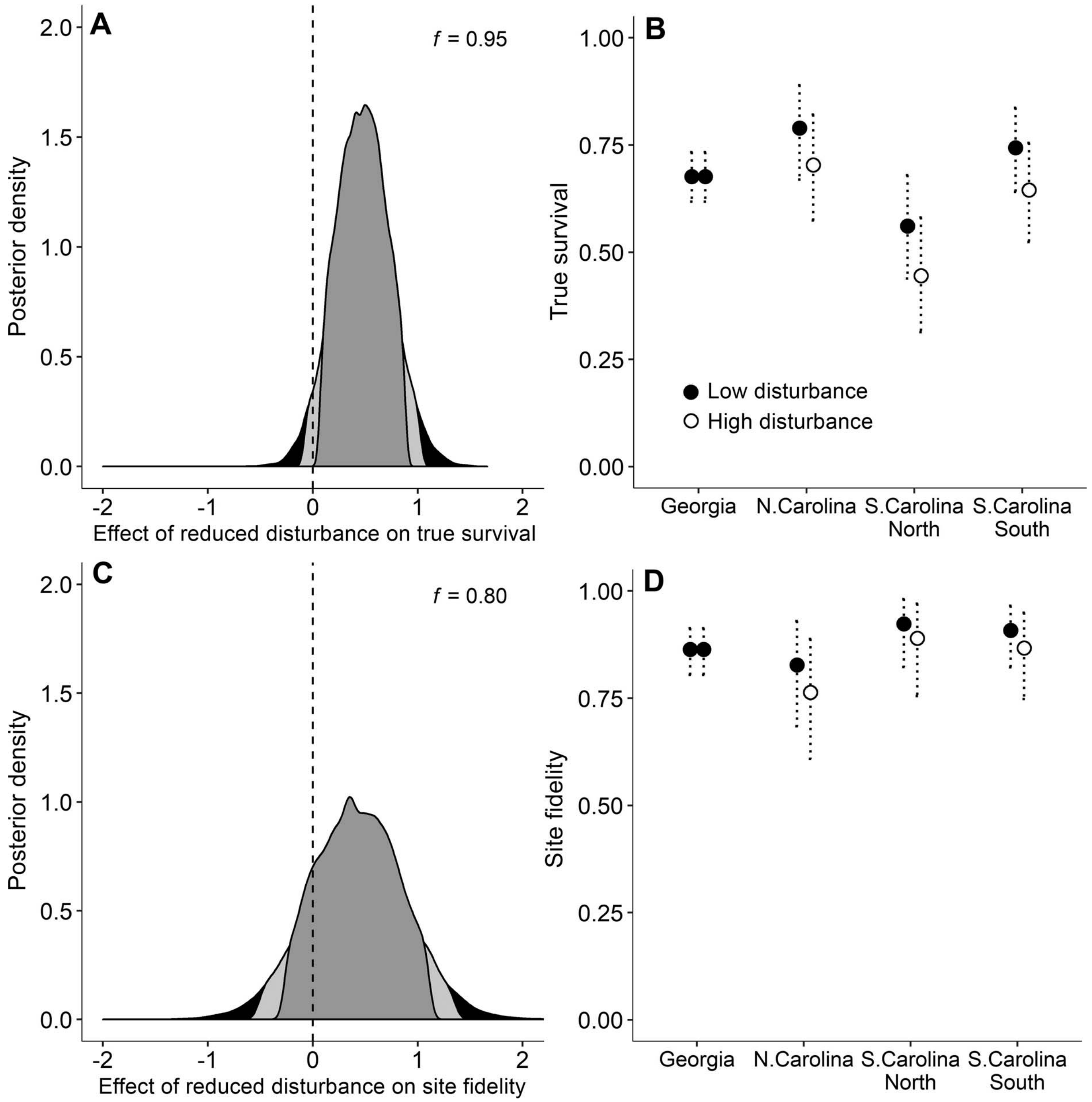

FIGURE 6. The posterior densities of the disturbance beta coefficient estimates (left column) and average point estimates for each study region (right column) for the (**A**, **B**) survival, and (**C**, **D**) site fidelity parameters for Piping Plovers associated with geographically proximate paired sites (see Table 1) experiencing high (white circles) or low (black circles) anthropogenic disturbance along the southeastern U.S. Atlantic Coast from 2012 to 2016. *f* represents the proportion of the posterior density distribution that is greater than zero (dashed vertical line). Error bars represent 95% Bayesian credible intervals. The shading of the posterior density distribution represents the extents of the 50–85% (dark gray), 85–95% (light gray), and 95–100% (black) Bayesian credible intervals.

demographic consequences during the nonbreeding season and beyond.

Although we found support for an impact of anthropogenic disturbance on the nonbreeding grounds on individual body condition and demography, the exact mechanism that drove these population dynamics remains unclear. Coastal modifications reduce benthic invertebrate abundance (Sobocinski et al. 2010) and alter sediment composition (Martin et al. 2005). Additionally, shorebird demographic rates in engineered habitats are often lower than those in more naturally created habitats (Cohen et al. 2009, Hunt et al. 2018). However, sites within our study area that experienced major shoreline modifications also experienced greater rates of recreational beach use. Thus, we cannot determine if Piping Plovers were in worse body condition due to decreases in invertebrate numbers following coastal modifications (Schlacher et al. 2012), or if increased disturbance reduced foraging efficiency

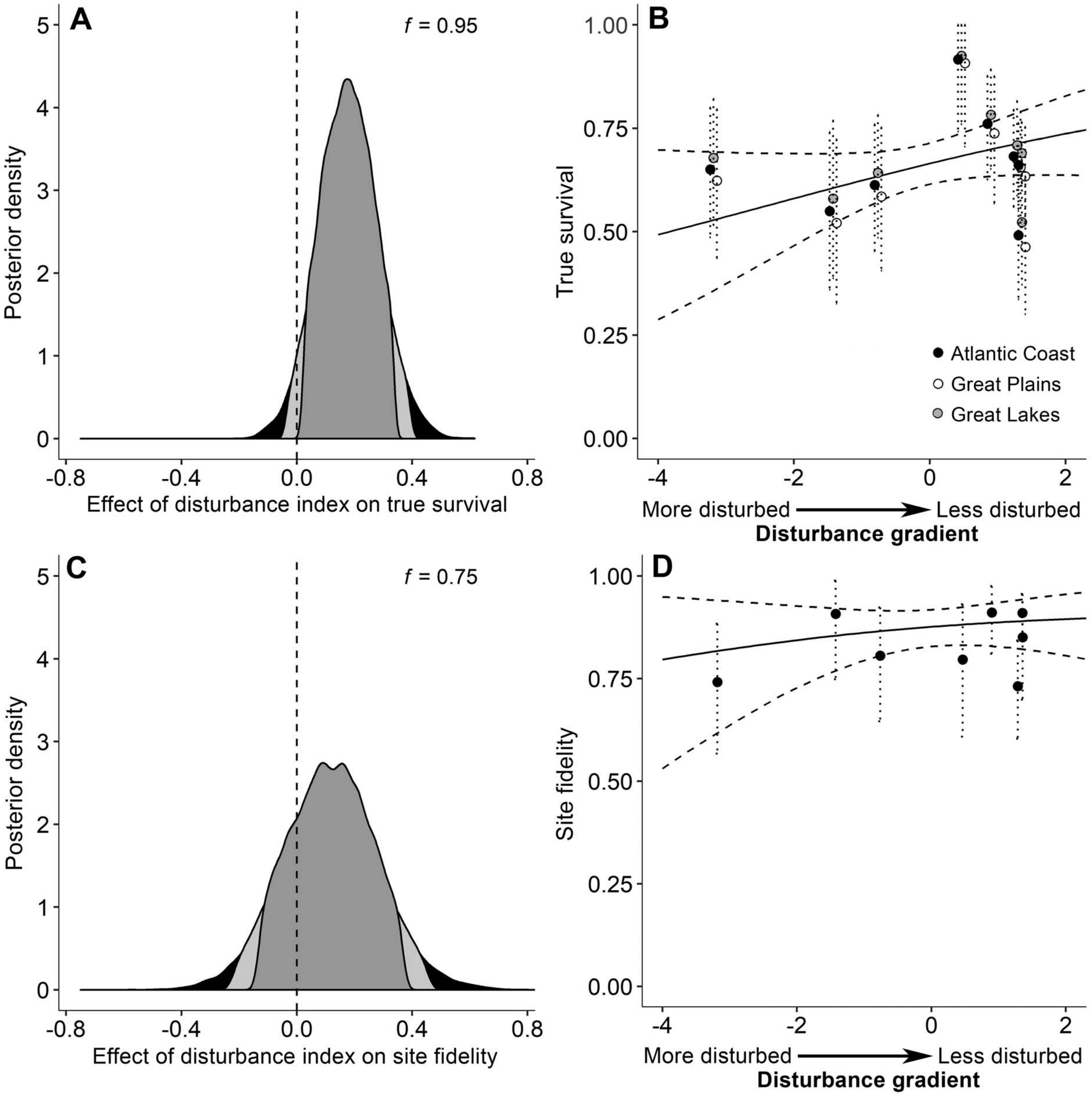

FIGURE 7. The posterior densities of the disturbance beta coefficient estimates (left column) and model-predicted covariate relationships (right column) for the (**A**, **B**) survival, and (**C**, **D**) site fidelity parameters from a model that assessed the influence of an index of anthropogenic disturbance on the true annual survival and nonbreeding site fidelity of Piping Plovers throughout the southeastern U.S. Atlantic Coast from 2012 to 2016. The *x*-axis in **B** and **D** (right column) represents an index of disturbance that was developed from a principle component analysis that considered human, vehicle, and dog activity, as well as the magnitude of previous shoreline modifications, and ranked sites from high (negative values) to low (positive values) disturbance. In panel **B**, the filled circles represent the mean true annual survival for individuals observed within the study area that bred in the Atlantic Coast (black), Great Plains (white), and Great Lakes (gray) regions. In panel **D**, point estimates represent the mean nonbreeding site fidelity rate for each site within the study area. Dashed lines and error bars represent 95% Bayesian credible intervals. Shading of the posterior density distribution (left column) represents the extents of the 50–85% (dark gray), 85–95% (light gray), and 85–100% (black) Bayesian credible intervals. *f* represents the proportion of the posterior density distribution that is greater than zero.

(Schlacher et al. 2013a). Nor can we determine causality, as the same pattern may also be observed if lower quality individuals are more common in disturbed sites.

Survival rates varied substantially among our less disturbed sites, indicating that local disturbance was not the only factor influencing nonbreeding demography. Most notably, survival rates for individuals associated with Deveaux Bank (DVB), a state-protected island, were substantially lower than those at all of the other sites that experienced low disturbance, but were similar to survival rates of individuals associated with the Kiawah and Seabrook islands (KSI), a nearby, highly disturbed area. We suspect that this was related to a relatively high exchange of individuals between KSI and DVB compared with the rest of the study areas. A larger proportion of birds were observed at least once at a given site's paired site at both DVB (~16% of individuals at DVB were observed at KSI) and KSI (~ 25% of individuals at KSI were observed at DVB) than at any of the other sites (Little Saint Simons Island: 6% vs. Cumberland Island National Seashore: 13%; Harbor Island: 4% vs Hilton Head Island: 5%; and Rich Inlet: 10% vs New Topsail Inlet: 8%). We speculate that the high level of exchange between KSI and DVB may have been related to a natural decline in Piping Plover habitat on DVB over the course of our study. Although the lack of independence among sites was not ideal, the alternative would have been to have paired sites that were more geographically, and potentially environmentally, disparate, which also may have reduced the potential for inference. Our approach, however, led to more conservative estimates, as the sharing of individuals among sites made it more difficult to observe pairwise differences in demographic rates associated with disturbance level.

Most vertebrate ecological research and conservation actions focus on organisms during their reproductive season (Marra et al. 2015), and Piping Plovers are no exception (Claassen et al. 2014). However, as migratory species often spend the majority of their life cycle away from their breeding grounds, conditions on the nonbreeding grounds or during migration can influence breeding season population dynamics by influencing the survival or condition of future breeders (Marra et al. 2015, Weithman et al. 2017). We found that disturbance on the nonbreeding grounds was negatively associated with both nonbreeding body condition and annual survival. Unless compensated through density-dependent mechanisms, these winter conditions should affect breeding population size.

Our study provides evidence that body condition and annual survival of wintering Piping Plovers are negatively associated with anthropogenic disturbance. During the nonbreeding season, the southeastern Atlantic Coast hosts >50% (relative to postbreeding abundance) of the critically endangered Great Lakes breeding population of Piping Plovers, with >30% occurring within our study area (Gratto-Trevor et al. 2012). Thus, anthropogenic disturbance in this area may disproportionally influence the population trajectory or sustainability of the Great Lakes Piping Plover population. Although site fidelity was slightly lower to disturbed areas relative to less disturbed areas, fidelity to nonbreeding grounds overall was high and largely similar to estimates of breeding site fidelity (Cohen et al. 2006, Cohen and Gratto-Trevor 2011, Catlin et al. 2015). Therefore, management objectives are not likely to be met if they are based on the expectation that Piping Plovers will move to better nonbreeding habitats if their current habitat is disturbed, despite the potential benefits of moving. However, management actions that identify and limit human access to critical foraging or roosting areas during the nonbreeding season may increase functionally available habitat, potentially improving body condition and survival rates of nonbreeding Piping Plovers. Annual survival rates of Piping Plovers at certain wintering sites were extremely low ($S < 0.50$) compared with published estimates of true survival ($S = 0.71$–0.76; Cohen et al. 2006, LeDee et al. 2010, Catlin et al. 2015). As hatch-year individuals consistently continue to be recruited into the wintering populations of these below-average sites, these areas apparently remain attractive sinks to Piping Plovers. Thus, conservation actions may be required to reduce the impact of these sink habitats on overall population dynamics.

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