2021

Impacts of extreme environmental disturbances on piping plover survival are partially moderated by migratory connectivity

Kristen S. Ellis

Michael J. Anteau

Francesca J. Cuthbert

Cheri L. Gratto-Trevor

Joel G. Jorgensen

See next page for additional authors

Authors

Kristen S. Ellis, Michael J. Anteau, Francesca J. Cuthbert, Cheri L. Gratto-Trevor, Joel G. Jorgensen, David J. Newstead, Larkin Powell, Megan M. Ring, Mark H. Sherfy, Rose J. Swift, Dustin L. Toy, and David N. Koons
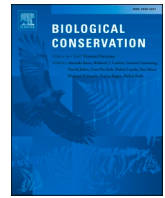
Impacts of extreme environmental disturbances on piping plover survival are partially moderated by migratory connectivity

Kristen S. Ellis [a],[*], Michael J. Anteau [a], Francesca J. Cuthbert [b], Cheri L. Gratto-Trevor [c], Joel G. Jorgensen [d], David J. Newstead [e], Larkin A. Powell [f], Megan M. Ring [a], Mark H. Sherfy [a], Rose J. Swift [a], Dustin L. Toy [a], David N. Koons [g]

[a] U.S. Geological Survey, Northern Prairie Wildlife Research Center, Jamestown, ND, USA
[b] University of Minnesota, Dept. of Fisheries, Wildlife and Conservation Biology, St. Paul, MN, USA
[c] Environment Canada, Prairie and Northern Wildlife Research Centre, Science and Technology Branch, Saskatoon, Saskatchewan, Canada
[d] Nebraska Game and Parks Commission, Nongame Bird Program, Lincoln, NE, USA
[e] Coastal Bend Bays and Estuaries Program, Corpus Christi, TX, USA
[f] University of Nebraska-Lincoln, School of Natural Resources, Lincoln, NE, USA
[g] Colorado State University, Dept. of Fish, Wildlife, and Conservation Biology, Graduate Degree Program in Ecology, Fort Collins, CO, USA

ARTICLE INFO

ABSTRACT

Effective conservation for listed migratory species requires an understanding of how drivers of population decline vary spatially and temporally, as well as knowledge of range-wide connectivity between breeding and nonbreeding areas. Environmental conditions distant from breeding areas can have lasting effects on the demography of migratory species, yet these consequences are often the least understood. Our objectives were to 1) evaluate associations between survival and extreme environmental disturbances at nonbreeding areas, including hurricanes, harmful algal blooms, and oil spills, and 2) estimate migratory connectivity between breeding and nonbreeding areas of midcontinental piping plovers (*Charadrius melodus*). We used capture and resighting data from 5067 individuals collected between 2002 and 2019 from breeding areas across the mid-continent, and nonbreeding areas throughout the Gulf of Mexico and southern Atlantic coasts of North America. We developed a hidden Markov multistate model to estimate seasonal survival and account for unobservable geographic locations. Hurricanes and harmful algal blooms were negatively associated with nonbreeding season survival, but we did not detect a similarly negative relationship with oil spills. Our results indicated that individuals from separate breeding areas mixed across nonbreeding areas with low migratory connectivity. Mixing among individuals in the nonbreeding season may provide a buffering effect against impacts of extreme events on any one breeding region. Our results suggest that understanding migratory connectivity and linking seasonal threats to population dynamics can better inform conservation strategies for migratory shorebirds.

Widespread declines in migratory bird populations (Rosenberg et al., 2019; Koleček et al., 2021; Warnock et al., 2021) emphasize the need for conservation strategies that address ongoing environmental changes and disturbances. The development of effective conservation strategies for most species requires an understanding of how drivers of population decline vary at different spatial and temporal scales (Runge et al., 2015; Rushing et al., 2017). This knowledge has additional relevance for mobile species, including migratory birds, that occupy separate geographic regions across the annual cycle where the type and intensity of stressors presumably varies. Studies on migratory birds have

predominantly focused on the geographic region that is occupied during the breeding season because of associations with fitness and recruitment (Faaborg et al., 2010; Rushing et al., 2017), and it is often more straightforward to implement conservation actions at breeding sites. Events occurring during nonbreeding periods of the annual cycle can induce carry-over effects into the breeding season (Harrison et al., 2011), and for most migratory birds, the breeding season encompasses a relatively small proportion of the annual cycle. Therefore, a holistic understanding of stressors and their impacts on migratory birds throughout the annual cycle is needed to develop rigorous conservation

plans (Martin et al., 2007; Faaborg et al., 2010; Marra et al., 2015).

Identifying and understanding the implications of stressors at appropriate spatial and temporal scales for migratory species requires a knowledge of linkages between spatially disjoint breeding and nonbreeding areas (i.e., migratory connectivity; Webster et al., 2002). If demographic rates, such as survival, vary between breeding and nonbreeding areas, estimates of migratory connectivity can provide vital insights into a species' population dynamics (Rockwell et al., 2017). Further, in situations where population trends are variable across a species' range, understanding the extent to which individuals from different areas co-occur seasonally can help focus conservation efforts. Sampling individuals at different points in the annual cycle can be challenging, particularly when the boundaries of a species' range have not been fully identified, or the range spans political boundaries (Marra et al., 2015). As a result, relatively few studies have estimated seasonal demography while accounting for connectivity in migratory species, although use of electronic tracking devices has led to an overall increase in our understanding of migratory connectivity for many bird species (McKinnon and Love, 2018).

As with many other bird taxa, migratory shorebirds (order Charadriiformes) present certain complexities in understanding migratory connectivity because of varied strategies within and among species. Variation exists in distances flown, stopover and wintering sites used, and population structure of nonbreeding groups (Haig et al., 1998; Colwell, 2010; Iwamura et al., 2014). Many species of migratory shorebirds depend on ocean shorelines and tidal marshes at some point in their annual cycle, and environmental conditions in these locations during nonbreeding periods may represent less-studied stressors on populations relative to conditions in breeding areas (Sutherland et al., 2012; Iwamura et al., 2014; Field et al., 2019). For example, extreme winter weather has been shown to alter population trajectories (Frederiksen et al., 2008), and climate change predictions indicate increasing severity and frequency of hurricanes and tropical storms (Bender et al., 2010). While assessments of direct impacts of hurricanes on migratory shorebirds have shown mixed results (Marsh and Wilkinson, 1991; Convertino et al., 2011; Saunders et al., 2014; Gibson et al., 2018a; Field et al., 2019), indirect effects may indeed lead to population growth when new habitat is created in breeding areas (Robinson et al., 2020a). Many studies evaluating impacts of hurricanes on shorebirds consider effects of a single storm event on a localized population (e.g., Marsh and Wilkinson, 1991; Gibson et al., 2018a), and a more robust understanding of these impacts would benefit from a spatial and temporal context that encompasses multiple storm events across a broad spatial scale.

Few studies have evaluated potential impacts of additional coastal disturbances on shorebirds, including oil spills (Henkel et al., 2012) and harmful algal blooms (van Deventer et al., 2012). Oil spills can directly impact birds that use coastal habitats by inducing lethal effects from chemical toxicity, suffocation, and reduction of insulation, flotation, or feather movement (Leighton, 1993). Shoreline habitats may become oiled when spills reach land and shorebirds using these habitats for foraging may, therefore, be susceptible to negative effects of oil. Previous research evaluating impacts of oiling on shorebird populations is limited, but highlights a diverse set of pathways through which shorebirds may be susceptible to contamination (Andres, 1997; Amirault-Langlais et al., 2007; Domínguez and Vidal, 2009; Henkel et al., 2012; Gibson et al., 2017). In addition to direct effects of oiling on shorebirds, long-term or indirect stressors related to reduced nutrient availability, body condition, and immune functions may represent nontrivial impacts on populations (Burger, 1997; Henkel et al., 2012).

Harmful algal blooms have been implicated as a source of mortality in marine mammals, turtles, birds, fish, and invertebrates (Burkholder et al., 2018; Landsberg, 2002). Coastlines within the Gulf of Mexico regularly experience blooms of the red tide dinoflagellate *Karenia brevis*, which produces potent neurotoxins, called brevetoxins (Landsberg et al., 2009). Ingestion of brevetoxins appears to be the primary route of exposure, yet the mechanisms behind the harmful effects of brevetoxins

through food webs are complex and continue to be the subject of investigations (Landsberg et al., 2009; Burkholder et al., 2018). *Karenia brevis* blooms have been associated with mass mortalities of marine birds (Shumway et al., 2003), and brevetoxins were present in the livers of dead shorebirds collected from coastal shorelines during an extended red tide event (van Deventer et al., 2012). Shorebirds primarily forage on benthic macroinvertebrates in surface sediments (Colwell, 2010), which could pose a risk if these prey species accumulate marine toxins (Kvitek and Bretz, 2005). Harmful algal blooms are predicted to further increase in frequency and expand in range in response to ocean warming and eutrophication (IPCC, 2019); thus, additional insight is needed to understand the potential impacts of harmful algal blooms on shorebird population dynamics.

Piping plovers (*Charadrius melodus*) are migratory shorebirds that periodically encounter coastal disturbances, as their known nonbreeding distribution falls along the Atlantic and Gulf of Mexico coasts of the United States, Mexico, and the Caribbean (Haig et al., 2005; Gratto-Trevor et al., 2012; Elliot-Smith et al., 2015). These coastal ecosystems serve as critical migratory stopover and nonbreeding habitats for many species of shorebirds, including species of conservation concern such as red knots (*Calidris canutus*) and American oystercatchers (*Haematopus palliatus*). Piping plovers are federally listed as threatened and endangered, with breeding populations in the Atlantic coast, Great Plains, and Great Lakes regions of North America (USFWS, 1985, 2009). Efforts by numerous research groups beginning in the 1990s to band and resight individual piping plovers has resulted in a considerable amount of information about populations in breeding areas (e.g., Roche et al., 2010; Cohen and Gratto-Trevor, 2011; Saunders et al., 2014; Catlin et al., 2015; Swift et al., 2020). Piping plovers present an ideal system to evaluate seasonal demography and impacts of environmental disturbances occurring on nonbreeding grounds because of the high proportion of marked birds, and relative ease of observing banded birds along shorelines by birders, and community and professional scientists. Previous research has shown an intermediate amount of overlap in nonbreeding areas among piping plovers breeding in the interior of North America but emphasized that certain breeding populations could be more impacted by extreme coastal disturbances in localized areas (Gratto-Trevor et al., 2012). Further, strong site fidelity and small movements by piping plovers within nonbreeding areas highlight the potential for exposure to extreme stressors (Drake et al., 2001; Cohen et al., 2008; Gratto-Trevor et al., 2016).

We used banding and resighting data from regional mark-recapture studies and a state-space modeling approach to address the following objectives: 1) evaluate the impacts of extreme coastal disturbances, including hurricanes, harmful algal blooms, and oil spills on piping plover nonbreeding season survival, 2) provide estimates of seasonal survival for piping plovers occupying midcontinental breeding areas and nonbreeding areas along the Atlantic and Gulf of Mexico coasts of the United States, and 3) estimate migratory connectivity between these spatially disjoint breeding and nonbreeding areas. Further, we were interested in whether concurrent estimates of seasonal survival were correlated among breeding and nonbreeding locations. Temporal correlation (i.e. synchrony) in adult piping plover survival among geographic regions has been documented previously and it was hypothesized that this was because of shared threats in nonbreeding areas (Roche et al., 2010). Synchrony in survival among regions could indicate common long-term trends, parallel fluctuations through time, or both (Lebreton et al., 1992; Grosbois et al., 2009). Events occurring in nonbreeding areas likely influence the number of individuals returning to breeding areas or can lead to cascading carry-over effects through subsequent seasons (Harrison et al., 2011). However, the influence of nonbreeding environmental conditions on population dynamics remains understudied for piping plovers (Roche et al., 2010), and for other shorebird species of conservation concern using similar nonbreeding habitats (Sutherland et al., 2012; Field et al., 2019). Consequently, additional research evaluating the impacts of extreme coastal

disturbances on seasonal survival with an understanding of migratory connectivity will inform a broader thinking of full-annual cycle conservation strategies for piping plovers, and provide insights into the impacts of extreme stressors on migratory shorebirds in nonbreeding areas.

1. Methods

1.1. Study areas and data collection

We used data from multiple mark-recapture studies between 2002 and 2019 representing piping plovers from four breeding areas and two populations (Great Lakes and Great Plains) within the midcontinent of North America (Fig. 1). Breeding areas included the Great Lakes and three regions within the Great Plains represented by Prairie Canada, Northern Great Plains, and Southern Great Plains. In the Great Lakes, piping plovers were monitored at breeding locations on Lakes Michigan, Superior, and Huron. Piping plovers within Prairie Canada were monitored in southern Saskatchewan at Big Quill Lake, Lake Diefenbaker, and wetlands within the Missouri Coteau. The Northern Great Plains included the Missouri River and its constructed reservoirs in central South Dakota through North Dakota, and alkali wetlands within the Missouri Coteau in North Dakota and Montana. The Southern Great Plains encompassed the Niobrara and lower and central Platte rivers. Habitats used by piping plovers at these breeding areas have been described previously (Prairie Canada: Cohen and Gratto-Trevor, 2011, Great Lakes: Ledee et al., 2010, Northern Great Plains: Anteau et al., 2012; Swift et al., 2021, Southern Great Plains: Sidle and Kirsch, 1993; Sherfy et al., 2012; Jorgensen et al., 2012). We included sampling years with adequate nonbreeding season detections for our analysis, but these

do not include all monitoring efforts at these breeding areas.

Surveys were conducted at breeding locations from May through July to uniquely mark unbanded adults and chicks, and to resight previously banded birds. Nesting piping plovers were captured during incubation on nests and chicks were caught by hand prior to fledging. Nonbreeding piping plovers in Texas were captured using whoosh nets, drop nets, or small cannon nets. Piping plovers were banded with unique combinations of United States Geological Survey (USGS) Bird Banding Laboratory metal bands, plastic color bands, or plastic color flags (which may have received unique alpha-numeric engravings) depending on the breeding area and year.

Sightings of banded piping plovers during the nonbreeding season were reported to banders by birders, nature photographers, and biologists from federal and state agencies and non-profit organizations. Nonbreeding season observations were collected and compiled via multiple sources including directed surveys (Gratto-Trevor et al., 2012), reports to the USGS Bird Banding Laboratory (Smith, 2013), photos of banded individuals on eBird (Sullivan et al., 2009), and iNaturalist. For our analysis, we divided the linear nonbreeding range of the Atlantic and Gulf of Mexico coastlines into regions such that each region had adequate observations to estimate demographic parameters. We considered three nonbreeding regions for our analysis, including 1) Texas and Mexico, 2) eastern Gulf of Mexico including Mississippi, Louisiana, Alabama, and the Gulf coast of Florida (hereafter eastern Gulf), and 3) Atlantic coast including North Carolina, South Carolina, Georgia, the Atlantic coast of Florida, and the Caribbean (Fig. 1). Observations of banded birds in Mexico and the Caribbean (primarily Cuba and The Bahamas) were sparse ($n = 62$ and 21, respectively), and spread over a wide geographic area. For example, resightings along the Gulf coast in Mexico ranged from the northern border of Mexico to the
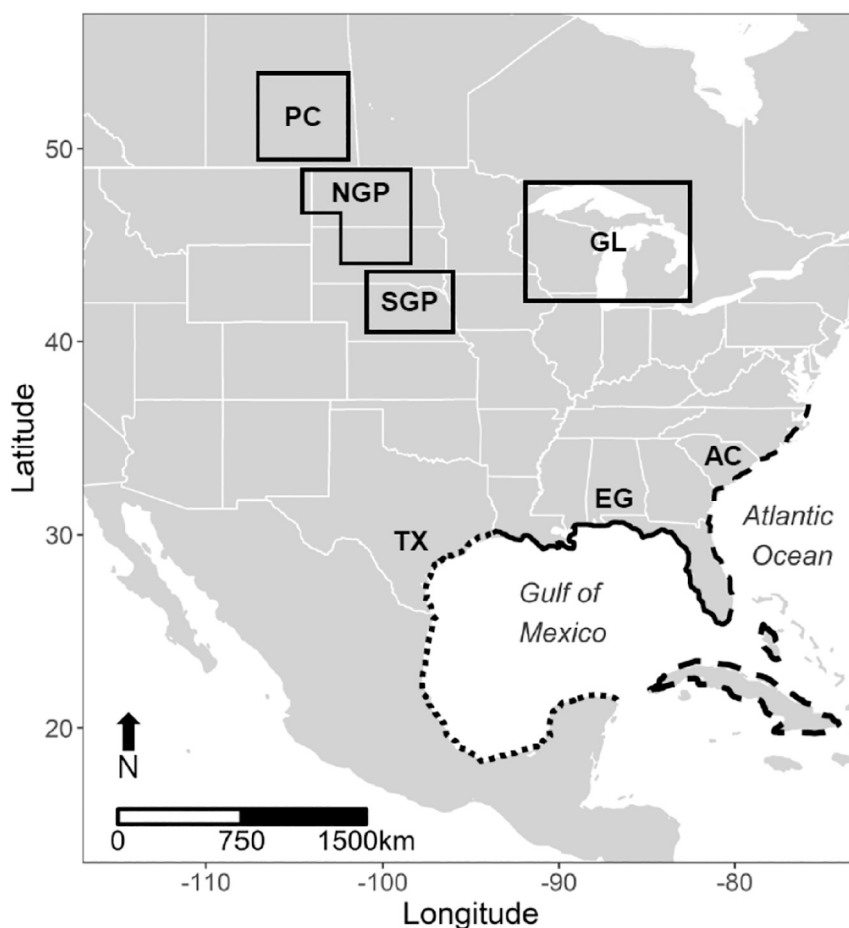
Fig. 1. Map of geographic states where piping plovers were banded and resighted. Breeding areas (represented by black polygons) and years of data included in our analysis were PC (Prairie Canada; 2002–2009), NGP (Northern Great Plains; 2012–2019), SGP (Southern Great Plains; 2010–2019), and GL (Great Lakes; 2010–2019). Data from nonbreeding areas (represented by black lines) between 2002 and 2019 encompassed the shorelines of TX (Texas and Mexico, dotted line), EG (Eastern Gulf of Mexico, solid line), and AC (Atlantic coast and Caribbean, dashed line). We estimated transition probabilities from each breeding region to each nonbreeding region (southbound), and from each nonbreeding region to each breeding region (northbound).

southern border within the state of Quintana Roo.

1.2. Environmental variables

We used publicly available information on hurricanes, harmful algal blooms, and oil spills obtained from the National Oceanic and Atmospheric Administration (NOAA) as covariates on survival in nonbreeding regions. We collected hurricane data from the HURDAT: Hurricane Re-Analysis Project package (Trice and Landsea, 2020) in program R 3.6.1 (Team, 2019). Rather than using the number of hurricane systems in each season, we used an index of hurricane exposure, defined as the number of 6-h periods where hurricane events (wind speed minimum of 64 kts) were present in nonbreeding regions. We included hurricanes that impacted the nonbreeding regions from 15 August – 31 December each year corresponding with approximate piping plover arrival in mid-August (primary hurricane season is from 1 June – 30 November). Seasonal hurricane exposure varied by nonbreeding region and was highest in the Atlantic coast ($\mu = 2.4 \pm 2.6$ SD, range $= 0$–9), compared to the eastern Gulf ($\mu = 1.4 \pm 1.7$ SD, range $= 0$–5) and Texas regions ($\mu = 1.3 \pm 1.7$ SD, range $= 0$–5). In addition, seasons without hurricanes occurred more often in Texas, and eastern Gulf regions ($n = 9$ and 8, respectively) and least often in the Atlantic coast region ($n = 5$).

We collected harmful algal bloom (HAB) data from the NOAA Harmful Algal Blooms Observing System (NOAA, 2014). This dataset contains HAB reports submitted by a network of organizations and agencies in Alabama, Florida, Mississippi, and Texas, and therefore does not encompass the entire nonbreeding range of piping plovers but includes the primary regions where HAB events are prevalent in the southeastern United States (NOAA, 2014). Across our study period, reports of water samples with >100,000 *Karenia brevis* cells/L (representing at least a medium bloom density which could lead to fish kills; NOAA, 2014) were highest in Florida ($n = 5171$; where 222 of those were on the Atlantic coast of Florida), compared to Gulf coasts in Texas ($n = 1100$), Mississippi ($n = 94$), and Alabama ($n = 45$). *Karenia brevis* HABs occur almost annually off the southwest coast of Florida, and less frequently elsewhere within the nonbreeding range of piping plovers (NOAA, 2014). These events vary in intensity and duration (from days to months), and typically occur from late-summer to early-spring (Burkholder et al., 2018). Given the distribution of HAB events, piping plovers occupying Texas and the Gulf coast of Florida during the nonbreeding season would have been more likely to experience negative effects from HAB events than birds in other nonbreeding locations. We estimated HAB intensity and prevalence in each nonbreeding region using the average *K. brevis* cells/L from sampled areas in each season (across all nonbreeding regions: $\mu = 5.8 \times 10^5 \pm 4.4 \times 10^6$ SD, range $= 0$–1.9×10^8 cells/L).

Lastly, we collected oil spill information from NOAA Emergency Response Division, Office of Response and Restoration, via IncidentNews (incidentnews.noaa.gov), which contains oil spill reports starting in 1985. We eliminated oil spills that were contained to open water and did not reach shorelines based on a combination of provided coordinates and incident descriptions. The number of oil spills was correlated with hurricanes (>0.6 Pearson's correlation coefficient) in the eastern Gulf region; therefore, we used the total estimated liters of oil released in each nonbreeding season in each region. Liters of oil spilled varied seasonally by nonbreeding region and was highest in the eastern Gulf ($\mu = 1.0 \times 10^7 \pm 2.5 \times 10^7$ SD, range $= 0$–8.4×10^7 L), compared to Texas ($\mu = 1.0 \times 10^6 \pm 3.3 \times 10^6$ SD, range $= 0$–1.3×10^7 L), and Atlantic coast ($\mu = 3.7 \times 10^3 \pm 8.6 \times 10^3$ SD, range $= 0$–2.7×10^4 L) regions. For both HAB and oil spills, we included events from 15 August – 31 March to correspond with approximate arrival and departure of piping plovers in nonbreeding areas.

1.3. Modeling framework

We developed a hidden Markov specification of a multistate capture-recapture model (Lebreton et al., 2009; McClintock et al., 2020) to estimate seasonal apparent survival (φ), resighting (p), and transition probabilities (ψ) for piping plovers in breeding and nonbreeding areas. We parameterized this model based on a hierarchical Bayesian multistate capture-recapture model (Kery and Schaub, 2011). Given the broad geographic extent where resightings occurred, we suspect estimates of φ are likely close to true survival, but we cannot rule out permanent emigration from study areas. Because data from breeding areas were not collected concurrently, and nonbreeding season observations were sparse in certain years, we implemented two sub-models with jointly estimated parameters. Data collected in Prairie Canada between 2002 and 2009 with corresponding nonbreeding season observations were included in the first sub-model. Data collected at the remaining three breeding regions (Northern Great Plains, Southern Great Plains, and Great Lakes) between 2010 and 2019 with corresponding nonbreeding season observations were included in the second sub-model.

We assigned all observations to one of 4 geographical states in the first sub-model (Prairie Canada and 3 nonbreeding regions), and to one of 6 geographical states in the second sub-model (Northern Great Plains, Southern Great Plains, Great Lakes, and 3 nonbreeding regions). These states were divided by season, where the breeding time period included observations during May – July from breeding states, and the nonbreeding time period included observations during October – February from nonbreeding states. We excluded observations from the migration phases of the annual cycle given the uncertainty of whether individuals were in transitional and stopover locations or final nonbreeding locations. Individuals were often observed multiple times in a single season, and occasionally in 2 or more different states ($n = 41$ occasions in multiple breeding states, $n = 33$ in multiple nonbreeding states). When individuals were observed in multiple states within a time period, we assigned the geographical state with the highest number of observations.

Each sub-model included an unobservable breeding state to account for the staggered study periods and to incorporate temporary emigration, given the seasonal design of our analysis (Kendall and Nichols, 2002; Schaub et al., 2004; Henle and Gruber, 2018). We fixed resighting probabilities in the unobservable breeding state to 0 to indicate that the state was unavailable for resighting (Schaub et al., 2004). It was also not possible to estimate unique survival probabilities for the unobservable state; therefore, we constrained such parameters to equal the average survival of the other breeding states. More specifically, survival for the unobservable breeding state equaled the average survival among Prairie Canada, Northern and Southern Great Plains, and the Great Lakes.

We restricted our analyses to after hatch year (AHY) birds because data from hatch-year birds were not collected consistently across sites or years. If piping plovers were first banded as chicks, we left-censored capture histories to begin with the first AHY detection, not including the first nonbreeding season. Because of the seasonal structure of our dataset, we included two encounter periods per year, and the study period was 17.5 years ending on a breeding season (first sub-model: 2002–2009, second sub-model: 2010–2019), providing 35 time intervals. Resightings occurred fairly continuously within seasons. Therefore, survival of breeding states represents survival from the mid-point of the breeding season to the mid-point of the nonbreeding season, and survival of nonbreeding states represents survival from the mid-point of the nonbreeding season to the mid-point of the breeding season.

We modeled all survival (ϕ) probabilities using a loglog-link, $\phi = exp(-exp(n))$, where n is the linear predictor (Ergon et al., 2018). The loglog-link on survival probabilities allowed us to compare hazard rates ($exp(n)$) between breeding and nonbreeding states using hazard ratios (i.e., relative differences in mortality; Ergon et al., 2018). Hazard rates are ratio-scaled intensities of mortality, and thus invariant to differing observation periods between breeding and nonbreeding seasons.

We estimated survival between breeding and nonbreeding time steps using temporal random effects and breeding state (bs)-specific means (μ_{bs}^{ϕ}). In the first sub-model, breeding survival was only estimated for

Prairie Canada, and temporal effects ε^{ϕ} on survival were assumed to be normally distributed with mean zero and variance $\sigma^{2,\,\phi}$. In the second sub-model, we assumed temporal effects ε^{ϕ} came from a multivariate normal distribution:

$$\phi_{t,bs} = exp\left(-exp\left(\mu_{bs}^{\phi} + \varepsilon_{t,bs}^{\phi}\right)\right); where\ \varepsilon_{t,bs}^{\phi} \sim MVN\left(0, \sum_{bs}\right)$$

where $\sum_{bs}$ was a 3×3 matrix with the diagonals containing the variances for Northern Great Plains, Southern Great Plains, and Great Lakes ($\sigma_{bs}^{2,\,\phi}$), and the off-diagonals containing the temporal covariances between them. With regard to breeding time steps, probabilities for nonbreeding states were fixed to 0.

For both sub-models, we estimated survival from nonbreeding to breeding time steps (i.e., nonbreeding survival) with temporal random effects and nonbreeding state (nbs)-specific means (μ_{nbs}^{ϕ}):

$$\phi_{t,nbs} = exp\left(-exp\left(\mu_{nbs}^{\phi} + \beta^{H} \times H_{nbs} + \beta^{A} \times A_{nbs} + \beta^{O} \times O_{nbs} + \varepsilon_{t,nbs}^{\phi}\right)\right); where\ \varepsilon_{t,nbs}^{\phi} \sim MVN\left(0, \sum_{nbs}\right)$$

where β^{H}, β^{A}, and β^{O} were coefficients associated with hurricane (H_{nbs}), harmful algal bloom (A_{nbs}), and oil spill predictors (O_{nbs}). Predictors were not collinear (<0.6 Pearson's correlation coefficient) and were respectively standardized by subtracting the mean and dividing by one standard deviation. $\sum_{nbs}$ was similarly a 3×3 matrix containing temporal variances ($\sigma_{nbs}^{2,\,\phi}$) and covariances among the nonbreeding states of origin. With regard to nonbreeding time steps, probabilities for breeding states were fixed to 0.

We modeled resight probabilities (p) for observable states with temporal random effects and state (s)-specific means (μ_{s}^{p}) on the logit scale:

$$logit\left(p_{t,s}\right) = \mu_{s}^{p} + \varepsilon_{t,s}^{p}; where\ \varepsilon_{t,s}^{p} \sim N\left(0, \sigma_{s}^{2,p}\right)$$

where $p_{t,\,s}$ is the probability that an individual in state s is observed on occasion t, given that it is alive at t. Because of differences in survey effort across states and years, temporal random effects $\varepsilon_{t,\,s}^{p}$ varied independently by state (s) and were assumed to be normally distributed with mean zero and variance $\sigma_{s}^{2,\,p}$. $p_{t,\,s}$ were estimated at appropriate alternating time intervals and were otherwise fixed to 0 for impossible time-steps corresponding to breeding and nonbreeding states. Because of sparse data in 2010 and 2011, we fixed resight probabilities in the Northern Great Plains to 0 in these time steps.

To address our last objective assessing migratory connectivity, we estimated transition probabilities between each breeding and nonbreeding state as an overall mean with no temporal variation (Fig. 1). Because the direction of migration is opposite in the breeding and nonbreeding seasons, unfeasible transitions were precluded depending on the season and state. In breeding season time steps, transitions from nonbreeding states and from breeding to breeding states (including fidelity probabilities) were fixed to 0. Therefore, we estimated six breeding to nonbreeding (southbound) transitions in the first sub-model (from Prairie Canada and the unobservable breeding state to three observable nonbreeding states), and 12 breeding to nonbreeding transitions in the second sub-model (from Northern Great Plains, Southern Great Plains, Great Lakes, and the unobservable breeding state to three observable nonbreeding states). In the nonbreeding season time steps, all transitions from breeding states and from nonbreeding to nonbreeding states (including fidelity probabilities) were fixed to 0. We estimated six nonbreeding to breeding transitions (northbound) in the first sub-model (from three nonbreeding states to Prairie Canada and the

unobservable breeding state), and 12 nonbreeding to breeding transitions in the second sub-model (from three nonbreeding states to Northern Great Plains, Southern Great Plains, Great Lakes, and the unobservable breeding state). Transition probabilities from each state were constrained with Dirichlet priors to ensure probabilities summed to one (Kery and Schaub, 2011).

We based our inference about migratory patterns on breeding to nonbreeding (southbound) transition probabilities, whereas nonbreeding to breeding (northbound) transition probabilities were primarily treated as nuisance parameters. Piping plovers display high site fidelity to breeding areas (Cohen et al., 2006; Cohen and Gratto-Trevor, 2011; Catlin et al., 2015; Swift et al., 2021), and relatively few individuals were first banded in nonbreeding areas ($n = 119$, in Texas). Using breeding to nonbreeding state transition probabilities, we measured the strength of migratory connectivity using methods described in Cohen et al. (2017), with the MigConnectivity package (Hostetler and Hallworth, 2021) in R. We calculated distance matrices between breeding states and between nonbreeding states using the centroids of each. We generated relative abundances for breeding states from data collected during an international piping plover census (Elliot-Smith et al., 2009). Values of migratory connectivity near 0 indicate low connectivity (mixing of individuals from distinct breeding areas in nonbreeding areas), whereas values near 1 indicate high connectivity (individuals from distinct breeding areas remain separated in the nonbreeding season; Cohen et al., 2017).

1.4. Estimation

We fit our model using Bayesian inference with JAGS 4.3 (Plummer, 2003) through the JAGSUI package (Kellner, 2019) in program R. We chose vague prior distributions for parameters, including a logistic distribution centered at 0 with scale parameter 1 for the logit of mean resight probabilities (Northrup and Gerber, 2018), normal distribution with mean 0 and standard deviation 0.75 for the loglog of mean survival probabilities, gamma distributions with shape and rate equal to 1 for mean transition probabilities and standard deviations of all random effect hyperparameters (Kery and Schaub, 2011), and uniform $[-1,1]$ for correlation coefficients using a separation strategy (Riecke et al., 2019; Robinson et al., 2020b). We assessed convergence using the Gelman-Rubin diagnostic $\hat{R}$ (Gelman et al., 1992) and visual inspection of trace plots. We generated 4 Markov chain Monte Carlo (MCMC) chains with random initial values using 50,000 iterations and discarded the first 10,000, at a thinning rate of 10, resulting in 16,000 saved iterations used to generate posterior distributions of parameters. These settings achieved convergence for estimated parameters as all $\hat{R} < 1.10$ and trace plots showed mixing among stationary MCMC chains. We present empirical means and 90% Bayesian credible intervals to summarize posterior distributions.

2. Results

We used encounter histories for 5067 uniquely marked AHY piping plovers, including newly marked adults, and resightings of previously marked adults and chicks. In the breeding areas, most birds were observed in the Northern Great Plains (63%), compared to 19% in Prairie Canada, 12% in the Southern Great Plains, and 6% in the Great Lakes. Piping plovers reliably returned to respective breeding areas, but

82 birds were observed in different breeding areas across breeding seasons, though none of these movements included birds from the Great Lakes (49% of movements were between the Northern and Southern Great Plains, 41% were between the Northern Great Plains and Prairie Canada, and 10% were between Prairie Canada and the Southern Great Plains). Among piping plovers that were observed in multiple breeding seasons, 68% were observed at least once in a nonbreeding area. Most individuals also returned to the same nonbreeding state, but 39 piping plovers were observed in different nonbreeding states across seasons. These interseason movements among nonbreeding states primarily occurred across border areas between Louisiana and Texas (64%), and the Gulf and Atlantic coasts of Florida (31%).

2.1. Resighting and survival

Resighting probabilities of piping plovers varied temporally across all geographic states (Fig. 2). Resighting probabilities in breeding states were lowest in Prairie Canada between 2006 and 2008. Resighting probabilities were generally <0.50 in nonbreeding states but were highest on the Atlantic coast in 2011, 2013, and 2019. Overall, resighting probabilities were variable between geographic states as temporal standard deviations on the logit-link scale were 0.51 (0.25–0.89) in Texas, 0.65 (0.13–1.42) in the eastern Gulf, and 0.57 (0.28–1.10) on the Atlantic coast, compared to 1.13 (0.69–1.79) in Prairie Canada, 0.29 (0.01–0.67) in the Northern Great Plains, 0.56 (0.02–1.54) in the Southern Great Plains, and 0.25 (0.03–0.57) in the Great Lakes.

Estimated survival among breeding states averaged 0.91 and was highest for individuals in the Great Lakes (0.96, 0.92–0.99), compared to 0.92 (0.87–0.97) in the Northern Great Plains, 0.83 (0.56–0.98) in the Southern Great Plains, and 0.88 (0.78–0.96) in Prairie Canada. Breeding state survival was consistently >0.80 in Prairie Canada, Great Lakes, and Northern Great Plains across our study period (Fig. 3). Survival among nonbreeding states averaged 0.81 across all nonbreeding areas and was highest for individuals in the Texas region (0.88, 0.77–0.95), compared to the Atlantic coast (0.81, 0.62–0.94) and the eastern Gulf (0.81, 0.64–0.92). The lowest estimates of nonbreeding season survival occurred in 2017 on the Atlantic coast (0.69, 0.43–0.87), and 2012 and 2015 on the eastern Gulf (0.76, 0.58–0.88; 0.74, 0.56–0.87, respectively; Fig. 3).

Temporal standard deviations on the link scale for survival probabilities were 0.52 (0.26–0.95) in Texas, 0.43 (0.19–0.82) in the eastern Gulf, and 0.51 (0.20–0.94) on the Atlantic coast in nonbreeding states,
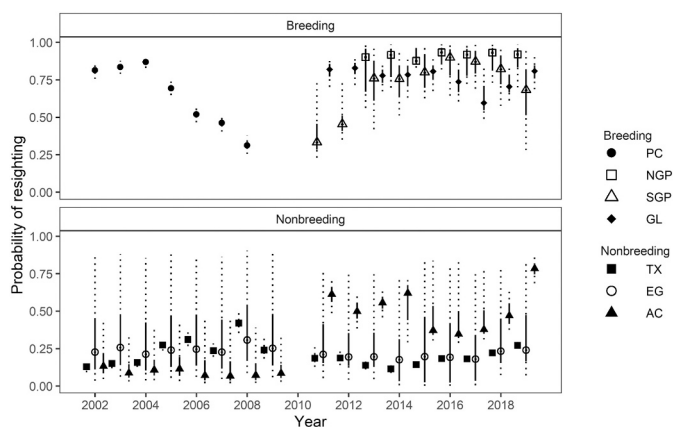

Fig. 3. Apparent survival probabilities of piping plovers (points indicate means, solid lines indicate 50% credible intervals, and dotted lines indicate 90% credible intervals) for breeding states (top), and nonbreeding states (bottom) between 2002 and 2019. NGP = Northern Great Plains, SGP = Southern Great Plains, PC = Prairie Canada, GL = Great Lakes, TX = Texas and Mexico, EG = Eastern Gulf of Mexico, AC = Atlantic coast and Caribbean.
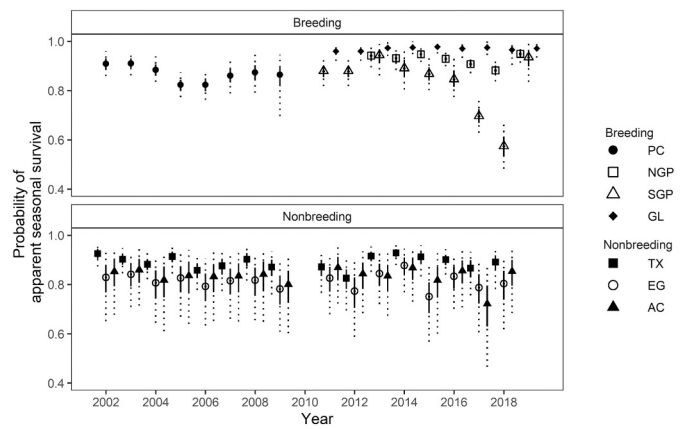
compared to 0.59 (0.09–1.50) in Prairie Canada, 0.58 (0.11–1.31) in the Northern Great Plains, 1.19 (0.59–2.21) in the Southern Great Plains, and 1.16 (0.04–3.63) in the Great Lakes. We found evidence for a small degree of temporal synchrony in survival between the Texas and eastern Gulf regions in the nonbreeding season (0.51, −0.08–0.94), and between the Northern and Southern Great Plains in the breeding season (0.53, −0.01–0.92; Fig. S1). Ratios of nonbreeding to breeding state hazard rates ranged from 10.50 (eastern Gulf: Great Lakes) to 1.17 (Texas: Prairie Canada), indicating that expected mortality events in nonbreeding seasons were consistently higher than in breeding seasons (Fig. S2).

Seasonal survival in nonbreeding regions was negatively related to the average *K. brevis* cells/L from sampled areas (95% of β^A was <0; Fig. 4). Hurricane intensity also elicited a negative effect on survival in nonbreeding regions (88% of β^H was <0; Fig. 4). We did not detect a negative effect of liters of oil spilled on survival as β^O was centered near 0 (0.02, −0.26–0.23; Fig. 4).
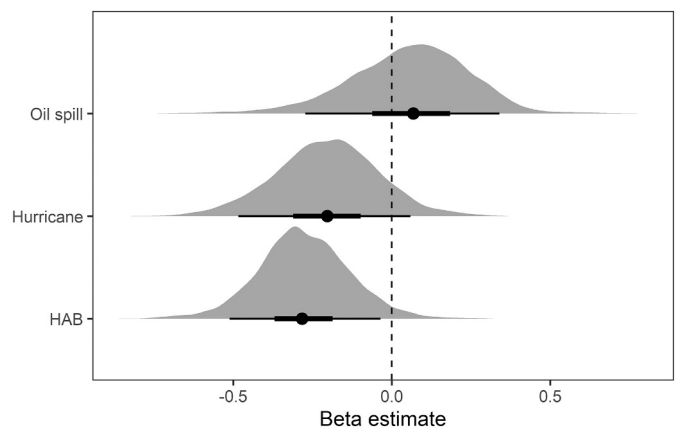

Fig. 2. Resighting probabilities of piping plovers (points indicate means, solid lines indicate 50% credible intervals, and dotted lines indicate 90% credible intervals) for breeding states (top), and nonbreeding states (bottom) between 2002 and 2019. NGP = Northern Great Plains, SGP = Southern Great Plains, PC = Prairie Canada, GL = Great Lakes, TX = Texas and Mexico, EG = Eastern Gulf of Mexico, AC = Atlantic coast and Caribbean.

Fig. 4. Posterior estimates of beta estimate effects on piping plover survival (points indicate means, thick solid lines indicate 50% credible intervals, and thin solid lines indicate 90% credible intervals) representing extreme environmental events, which varied seasonally and among nonbreeding states, including HAB (harmful algal blooms measured by *K. brevis* cells/L in sampled areas), hurricane (hurricane intensity measured as the number of 6-h periods where hurricane events were present in nonbreeding regions), and oil spill (total L of oil released). The vertical dashed line indicates an effect size of 0.

Table 1
Piping plover migratory connectivity estimated as transition probabilities for fall (from breeding to nonbreeding states) and spring (from nonbreeding to breeding states) migration. The origin is shown in the first column while the destination is shown in the other columns, therefore all rows sum to 1. Transition probabilities (with 90% Bayesian credible intervals) indicate the mean across the study periods where the first sub-model encompassed 2002–2009 and the second sub-model encompassed 2010–2019. PC = Prairie Canada, UB = unobservable breeding state, TX = Texas and Mexico, EG = Eastern Gulf of Mexico, AC = Atlantic coast, NGP = Northern Great Plains, SGP = Southern Great Plains, GL = Great Lakes.

First sub-model				
Origin	Transition	Destination		
		PC	UB	
TX	Spring	0.91 (0.69–0.99)	0.09 (0.01–0.31)	
EG	Spring	0.79 (0.56–0.99)	0.21 (0.01–0.44)	
AC	Spring	0.58 (0.35–0.99)	0.42 (0.01–0.65)	
Origin	Transition	Destination		
		TX	EG	AC
PC	Fall	0.64 (0.17–0.90)	0.25 (0.05–0.75)	0.11 (0.04–0.47)
UB	Fall	0.29 (0.01–0.89)	0.30 (0.03–0.66)	0.41(0.06–0.71)

Second sub-model					
Origin	Transition	Destination			
		NGP	SGP	GL	UB
TX	Spring	0.70 (0.55–0.88)	0.11 (0.06–0.18)	0.02 (0.01–0.05)	0.17 (0.01–0.29)
EG	Spring	0.50 (0.39–0.60)	0.11 (0.07–0.18)	0.31 (0.18–0.44)	0.08 (0.01–0.19)
AC	Spring	0.15 (0.08–0.24)	0.17 (0.09–0.26)	0.66 (0.52–0.76)	0.02 (0.01–0.05)
Origin	Transition	Destination			
		TX	EG	AC	
NGP	Fall	0.83 (0.72–0.89)	0.12 (0.07–0.20)	0.05 (0.03–0.12)	
SGP	Fall	0.60 (0.44–0.71)	0.20 (0.12–0.33)	0.20 (0.11–0.31)	
GL	Fall	0.04 (0.02–0.08)	0.28 (0.20–0.37)	0.68 (0.58–0.77)	
UB	Fall	0.68 (0.03–0.97)	0.27 (0.01–0.91)	0.05 (0.01–0.17)	

2.2. Migratory transitions

Individuals that were observed in Prairie Canada, Northern Great Plains, and the Southern Great Plains had high probabilities of migrating to the Texas and Mexico coasts in the nonbreeding season (0.64, 0.83, and 0.60, respectively; Table 1); whereas, individuals from the Great Lakes had high probabilities of migrating to the Atlantic coast (0.68). Migration probabilities from the unobserved breeding state in the first sub-model were relatively split among nonbreeding states, whereas migration probabilities to the Texas and Mexico coasts were higher in the second sub-model (0.68). Using breeding to nonbreeding (southbound) transition probabilities for observable breeding states, our results indicated low migratory connectivity (migratory connectivity = 0.13).

3. Discussion

We assessed migratory patterns and seasonal and geographical state-specific survival probabilities for threatened (Great Plains) and endangered (Great Lakes) piping plovers that breed within the midcontinent of North America. Our assessment revealed that seasonal survival varied spatially and temporally and was impacted by hurricanes and harmful algal blooms occurring in the nonbreeding season. Seasonal survival was generally more variable in the nonbreeding season (encompassing northbound migration) than the breeding season (encompassing southbound migration). Previous work on piping plovers in the nonbreeding season has indicated that Great Lakes breeding birds primarily winter on the Atlantic coast and Gulf coast of Florida, whereas Great Plains and Prairie Canada birds primarily winter on the Gulf of Mexico (Haig and Oring, 1988; Haig et al., 2005; Stucker et al., 2010; Gratto-Trevor et al., 2012). The transition probabilities we observed agree with this work, despite potential limitations in our inability to separate nonbreeding areas into finer-scale segments.

Migratory connectivity between midcontinental breeding regions was low (0.13), which agrees with previous findings of piping plover

migratory connectivity of breeding sites within the central flyway (0.08), although range-wide connectivity was higher (0.45; Gibson et al., 2019). This assessment further suggested that variation in the migratory potential of individuals may contribute to low connectivity (Gibson et al., 2019). If driven by individual variation, low migratory connectivity may indirectly benefit a species that encounters periodic mortality events (e.g., hurricanes) such that no single breeding population is disproportionately affected. Thus, our study agrees with previous work highlighting the importance of identifying the amount of mixing among individuals from separate breeding areas so that critical nonbreeding habitats can be maintained, particularly for small populations like those in the Great Lakes.

We found differences in apparent seasonal survival of piping plovers among geographic regions; however, there was evidence of temporal similarities between the Northern and Southern Great Plains. The synchronous survival probabilities we observed may indicate that individuals in these regions experience similar environmental conditions and mortality risk. While we do not fully understand the mechanisms driving these temporal similarities, of note is that our estimates do not provide evidence of broad scale declines in adult survival across geographic regions, which have been identified in earlier estimates for piping plovers (Roche et al., 2010; Ledee et al., 2010). Further, we found that estimates of average annual survival (product of seasonal estimates) varied between 0.68 and 0.82, which are comparable to previously published estimates of adult annual survival (0.71–0.85; Cohen et al., 2006; Ledee et al., 2010; Cohen and Gratto-Trevor, 2011; Catlin et al., 2015; Saunders et al., 2018; Swift et al., 2021). Because adult piping plovers show a high degree of site fidelity to breeding and nonbreeding areas (Drake et al., 2001; Cohen et al., 2006; Cohen et al., 2008; Cohen and Gratto-Trevor, 2011; Catlin et al., 2015; Swift et al., 2021) and our study encompassed a large region of observations and incorporated temporary emigration through the use of an unobservable state, we suspect that estimated apparent survival approaches 'true' adult survival. We did not explicitly test a linear effect for time and while linear trends can represent valuable simplifications, they often cannot describe

how survival varies through time (Kery et al., 2006; Dinsmore, 2008). However, our results do not appear to support overall declines in adult survival, despite concerns about increasing frequency of disturbances (e. g., Atlantic hurricanes; Bender et al., 2010) in nonbreeding areas.

Limited empirical research has been conducted assessing the impacts of HAB events on shorebird populations, yet mortalities and illness of many species of coastal birds from brevetoxicosis are routinely acknowledged by local managers and biologists (Fauquier et al., 2013; Burkholder et al., 2018). We found a decrease in nonbreeding season survival when *K. brevis* cells/L from sampled areas was high, which is consistent with research on piping plovers in Florida (Tuma, 2020). The primary route of exposure for shorebirds to brevetoxins produced by *K. brevis* is generally thought to be through ingestion from both food and water (Pierce and Henry, 2008; Landsberg et al., 2009). Shorebird diets tend to reflect the availability of macroinvertebrates in the surface sediment, including polychaetes, amphipods, molluscs, and insects (Shaffer and Laporte, 1994; Colwell, 2010). Macroinvertebrates have been shown to accumulate brevetoxins in their tissues during *K. brevis* HAB events and may act as sources for transferring toxins within the food web (Bricelj et al., 2012; Echevarria et al., 2012). Shorebird species that have specialist diets of filter-feeding organisms, may experience increased toxic exposure because of accumulated concentrations of brevetoxins in the tissues of these organisms (Landsberg et al., 2009). However, following a widespread and prolonged *K. brevis* HAB in Florida in 2005, radical changes in the structures of coastal communities occurred (Dupont et al., 2010), and several species of small-bodied shorebirds were observed foraging on fish carcasses (van Deventer et al., 2012). Indeed, tissue samples of fish carcasses collected during this *K. brevis* HAB contained levels of brevetoxins that would likely be lethal to a bird weighing less than 60 g (adult piping plover weight range: 43–63 g; Elliot-Smith and Haig, 2020), and tissues of shorebird carcasses similarly contained elevated levels of brevetoxins (van Deventer et al., 2012). Opportunistic foraging by shorebirds on fish carcasses containing elevated levels of toxins, while relatively uncommon (Gochfeld and Burger, 1980), could occur when macroinvertebrate communities are disrupted by HAB events (Landsberg et al., 2009), and act as an alternate route by which shorebirds are exposed to harmful toxins. Nonetheless, our results suggest that *K. brevis* blooms may represent a meaningful source of mortality for adult piping plovers during the nonbreeding season. Future conservation planning may benefit from considering these events, and potentially involve an evaluation of the effectiveness of local efforts to remove fish carcasses from beaches during HAB events.

Hurricanes have been associated with immediate population declines of coastal avian species (Raynor et al., 2013). Given predicted increasing frequency and intensity of hurricanes in the Atlantic Ocean under ongoing climate change (Bender et al., 2010), a better understanding of the impacts of hurricanes on species of conservation concern is warranted. Using data from a broad spatial region that experienced multiple hurricane systems with variable intensities, we found that hurricanes had a negative effect on piping plover survival. Hurricane frequency was not influential on the annual survival of piping plovers breeding in New Jersey (Stantial, 2020). As such, hurricanes may differentially affect coastally-breeding piping plovers compared to interior populations. A study involving American oystercatchers during the nonbreeding season similarly indicated that weekly apparent survival was not affected by a major hurricane event on the Atlantic coast (Gibson et al., 2018a). However, estimates of piping plover survival that were shown to be negatively associated with hurricane intensity, including those from Saunders et al. (2014) and our study, encompassed migratory periods, potentially suggesting that the negative effects of hurricanes are partially realized during northbound migration, possibly through carry-over effects. While it is likely that the factors contributing to negative associations between hurricanes and shorebird survival are complex, hurricanes can cause lasting impacts on entire ecosystems, including reduced macroinvertebrate abundance and diversity (Patrick

et al., 2020). Individuals surviving the direct effects of hurricanes may experience reduced food availability or be displaced to suboptimal foraging habitats and, therefore, begin spring migration in poor body condition (Gill et al., 2001; Fernández et al., 2003; Morrison et al., 2007). Life histories of migratory shorebirds have likely been shaped by naturally occurring extreme events during the nonbreeding season, and we do not fully understand the implications of reduced nonbreeding season survival, or an increase in the frequency of extreme events on population trajectories.

We failed to detect an effect of oil spills on seasonal survival, and our results are consistent with previous work conducted at a much finer spatial scale than ours addressing the 2010 Deepwater Horizon oil spill, which found little evidence of an effect of oil on local beach persistence or survival for piping plovers (Gibson et al., 2017). While we lacked sufficient data to estimate survival during this time period in our study, it is important to note that essentially all piping plovers had departed for breeding in northern latitudes from the oil-affected beaches prior to the time oil from the Deepwater Horizon spill reached nonbreeding habitats. Gibson et al. (2017) suggest that piping plovers were likely at less of a risk to the Deepwater Horizon event relative to other avian species that breed in the Gulf of Mexico. However, coastal environments are subject to small, regularly occurring oil spills (Henkel et al., 2012). Perhaps because these oil spills receive relatively less attention, limited research exists evaluating the impacts of smaller, more frequent oil spills on shorebird populations. Experimental evidence has shown that small amounts of oil exposure can lead to increased energy expenditure during flights (Maggini et al., 2017) and reduced fueling abilities (Bursian et al., 2017; Bianchini and Morrissey, 2018) in migratory shorebirds, and reduced fueling ability has been associated with population declines (Baker et al., 2004). Oil contaminants can persist in ecosystems for decades, and the long-term effects of this persistence on avian species is largely unknown (Henkel et al., 2012). Although we did not detect an effect of oil spills on piping plover survival, our study does not necessarily indicate they have no effect, potentially because we assessed short-term impacts over a large spatial extent. Assessing the long-term survival of impacted individuals at varying levels of oil exposure is challenging, and often ad hoc due to the unpredictable nature of oil spills. Therefore, continued monitoring in nonbreeding areas may provide useful data for understanding the long-term effects of oil pollution on the survival of migratory shorebirds.

Coastal ecosystems support diverse and dynamic assemblages of species yet are increasingly being affected by stressors including climate change (e.g., sea level rise and increased frequency of extreme weather), pollution (e.g., oil spills), and habitat loss from human activities. For example, ecosystem changes that support increasing occurrences of HAB events include nutrient pollution from agriculture operations, aquaculture development, changes in water flows, and increased water temperatures (Burkholder et al., 2018). The challenges involved in managing upstream nutrient outputs and HAB events will continue to be complex, however, vulnerable species dependent on coastal ecosystems would likely benefit from such management. Our study demonstrates how an understanding of migratory connectivity and seasonal survival can inform the conservation of imperiled shorebird populations. While we did find temporal variation in nonbreeding season survival, we did not detect substantial differences in average seasonal survival among nonbreeding regions. This finding, along with our assessment of migratory connectivity, suggests that no breeding population or region was more susceptible than another to high adult mortality in the nonbreeding season during our study period. Additional environmental factors, that we did not incorporate, have been shown to impact adult survival during the nonbreeding season, such as anthropogenic disturbances (Gibson et al., 2018b) or the abundance of predators (Saunders et al., 2014). Therefore, understanding the combined contributions of varying threats to nonbreeding season survival on piping plover population dynamics and recovery will be essential for developing further conservation actions at appropriate temporal and spatial scales.

CRediT authorship contribution statement

Kristen S. Ellis: Formal analysis, Writing – original draft. **Michael J. Anteau:** Conceptualization, Funding acquisition, Writing – review & editing. **Francesca J. Cuthbert:** Data curation, Investigation, Writing – review & editing. **Cheri L. Gratto-Trevor:** Data curation, Investigation, Writing – review & editing. **Joel G. Jorgensen:** Data curation, Investigation, Writing – review & editing. **David J. Newstead:** Data curation, Investigation, Writing – review & editing. **Larkin A. Powell:** Data curation, Investigation, Writing – review & editing. **Megan M. Ring:** Data curation, Investigation, Writing – review & editing. **Mark H. Sherfy:** Conceptualization, Investigation, Writing – review & editing. **Rose J. Swift:** Conceptualization, Writing – review & editing. **Dustin L. Toy:** Data curation, Investigation, Writing – review & editing. **David N. Koons:** Formal analysis, Writing – review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgments

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2021.109371.

References

Amirault-Langlais, D.L., Thomas, P.W., McKnight, J., 2007. Oiled piping plovers (*Charadrius melodus melodus*) in eastern Canada. Waterbirds 30, 271–274.

Andres, B.A., 1997. The Exxon Valdez oil spill disrupted the breeding of black oystercatchers. J. Wildl. Manag. 1322–1328.

Anteau, M.J., Sherfy, M.H., Wiltermuth, M.T., 2012. Selection indicates preference in diverse habitats: a ground-nesting bird (*Charadrius melodus*) using reservoir shoreline. PloS One 7, e30347.

Baker, A.J., Gonzalez, P.M., Piersma, T., Niles, L.J., de Lima Serrano do Nascimento, I., Atkinson, P.W., Clark, N.A., Minton, C.D.T., Peck, M.K., Aarts, G., 2004. Rapid population decline in Red Knots: fitness consequences of decreased refuelling rates and late arrival in Delaware Bay. Proc. R. Soc. B Biol. Sci. 271, 875–882.

Bender, M.A., Knutson, T.R., Tuleya, R.E., Sirutis, J.J., Vecchi, G.A., Garner, S.T., Held, I. M., 2010. Modeled impact of anthropogenic warming on the frequency of intense Atlantic hurricanes. Science 327, 454–458.

Bianchini, K., Morrissey, C.A., 2018. Polycyclic aromatic hydrocarbon exposure impairs pre-migratory fuelling in captively-dosed sanderling (*Calidris alba*). Ecotoxicol. Environ. Saf. 161, 383–391.

Bricelj, V.M., Haubois, A.-G., Sengco, M.R., Pierce, R.H., Culter, J.K., Anderson, D.M., 2012. Trophic transfer of brevetoxins to the benthic macrofaunal community during a bloom of the harmful dinoflagellate *Karenia brevis* in Sarasota Bay, Florida. Harmful Algae 16, 27–34.

Burger, J., 1997. Effects of oiling on feeding behavior of sanderlings and semipalmated plovers in New Jersey. Condor 99, 290–298.

Burkholder, J., Shumway, S.E., Glibert, P.M., 2018. Food web and ecosystem impacts of harmful algae. In: Harmful Algal Blooms. Wiley-Blackwell, Hoboken, NJ, USA, pp. 243–336.

Bursian, S.J., Alexander, C.R., Cacela, D., Cunningham, F.L., Dean, K.M., Dorr, B.S., Ellis, C.K., Godard-Codding, C.A., Guglielmo, C.G., Hanson- Dorr, K.C., Harr, K.E., Healy, K.A., Hooper, M.J., Horak, K.E., Isanhart, J.P., Kennedy, L.V., Link, J.E., Maggini, I., Moye, J.K., Perez, C.R., Pritsos, C.A., Shriner, S.A., Trust, K.A., Tuttle, P. L., 2017. Overview of avian toxicity studies for the Deepwater Horizon natural resource damage assessment. Ecotoxicol. Environ. Saf. 142, 1–7.

Catlin, D.H., Fraser, J.D., Felio, J.H., 2015. Demographic responses of piping plovers to habitat creation on the Missouri river. Wildl. Monogr. 192, 1–42.

Cohen, J.B., Gratto-Trevor, C., 2011. Survival, site fidelity, and the population dynamics of piping plovers in Saskatchewan. J. Field Ornithol. 82, 379–394.

Cohen, J.B., Fraser, J.D., Catlin, D.H., 2006. Survival and site fidelity of piping plovers on Long Island, New York. J. Field Ornithol. 77, 409–417.

Cohen, J.B., Karpanty, S.M., Catlin, D.H., Fraser, J.D., Fischer, R.A., 2008. Winter ecology of piping plovers at Oregon inlet, North Carolina. Waterbirds 31, 472–479.

Cohen, E.B., Hostetler, J.A., Hallworth, M.T., Rushing, C.S., Sillett, T.S., Marra, P.P., 2017. Quantifying the strength of migratory connectivity. Methods Ecol. Evol. 9, 513–524.

Colwell, M.A., 2010. Shorebird ecology, conservation, and management. University of California Press, Oakland, CA, USA.

Convertino, M., Elsner, J.B., Muñoz-Carpena, R., Kiker, G.A., Martinez, C.J., Fischer, R. A., Linkov, I., 2011. Do tropical cyclones shape shorebird habitat patterns? Biogeoclimatology of snowy plovers in Florida. PLoS One 6, e15683.

Dinsmore, S.J., 2008. Influence of drought on annual survival of the mountain plover in Montana. Condor 110, 45–54.

Domínguez, J., Vidal, M., 2009. Factors affecting plumage oiling levels in a Kentish plover *Charadrius alexandrinus* population after a major oil spill. Acta Ornithol. 44, 119–126.

Drake, K.R., Thompson, J.E., Drake, K.L., Zonick, C., 2001. Movements, habitat use, and survival of nonbreeding piping plovers. Condor 103, 259–267.

Dupont, J.M., Hallock, P., Jaap, W.C., 2010. Ecological impacts of the 2005 red tide on artificial reef epibenthic macroinvertebrate and fish communities in the eastern Gulf of Mexico. Mar. Ecol. Prog. Ser. 415, 189–200.

Echevarria, M., Naar, J.P., Tomas, C., Pawlik, J.R., 2012. Effects of *karenia brevis* on clearance rates and bioaccumulation of brevetoxins in benthic suspension feeding invertebrates. Aquat. Toxicol. 106–107, 85–94.

Elliot-Smith, E., Haig, S.M., 2020. Piping plover (*Charadrius melodus*). In: Birds World. Cornell Lab of Ornithology, Ithaca, NY, USA.

Elliot-Smith, E., Haig, S.M., Powers, B.M., 2009. Data from the 2006 International Piping Plover Census: U.S. Geological Survey Data Series 426, 332 p.

Elliott-Smith, E., Bidwell, M., Holland, A.E., Haig, S.M., 2015. Data from the 2011 International Piping Plover Census: U.S. Geological Survey Data Series, 922, p. 296. https://doi.org/10.3133/ds922.

Ellis, K.S., Anteau, M.J., Ring, M.M., Sherfy, M.H., Swift, R.J., Toy, D.L., 2021. Impacts of extreme environmental disturbances on survival of piping plovers breeding in the Great Plains, and wintering along the Gulf of Mexico and Atlantic Coasts, 2012 – 2019. In: U.S. Geological Survey data release. https://doi.org/10.5066/P9LHWAOQ.

Ergon, T., Borgan, O., Nater, C.R., Vindenes, Y., 2018. The utility of mortality hazard rates in population analyses. Methods Ecol. Evol. 9, 2046–2056.

Faaborg, J., Holmes, R.T., Anders, A.D., Bildstein, K.L., Dugger, K.M., Gauthreaux Jr., S. A., Heglund, P., Hobson, K.A., Jahn, A.E., Johnson, D.H., et al., 2010. Conserving migratory land birds in the New World: do we know enough? Ecol. Appl. 20, 398–418.

Fauquier, D.A., Flewelling, L.J., Maucher, J.M., Keller, M., Kinsel, M.J., Johnson, C.K., Henry, M., Gannon, J.G., Ramsdell, J.S., Landsberg, J.H., 2013. Brevetoxicosis in seabirds naturally exposed to *Karenia brevis* blooms along the central west coast of Florida. J. Wildl. Dis. 49, 246–260.

Fernández, G., de la Cueva, H., Warnock, N., Lank, D.B., 2003. Apparent survival rates of Western sandpiper (*Calidris mauri*) wintering in Northwest Baja California, Mexico. Auk 120, 55–61.

Field, C.R., Ruskin, K.J., Cohen, J.B., Hodgman, T.P., Kovach, A.I., Olsen, B.J., Shriver, W.G., Elphick, C.S., 2019. Framework for quantifying population responses

to disturbance reveals that coastal birds are highly resilient to hurricanes. Ecol. Lett. 22, 2039–2048.

Frederiksen, M., Daunt, F., Harris, M.P., Wanless, S., 2008. The demographic impact of extreme events: stochastic weather drives survival and population dynamics in a long-lived seabird. J. Anim. Ecol. 77, 1020–1029.

Gelman, A., Rubin, D.B., et al., 1992. Inference from iterative simulation using multiple sequences. Stat. Sci. 7, 457–472.

Gibson, D., Catlin, D.H., Hunt, K.L., Fraser, J.D., Karpanty, S.M., Friedrich, M.J., Bimbi, M.K., Cohen, J.B., Maddock, S.B., 2017. Evaluating the impact of man-made disasters on imperiled species: piping plovers and the Deepwater Horizon oil spill. Biol. Conserv. 212, 48–62.

Gibson, D., Riecke, T.V., Keyes, T., Depkin, C., Fraser, J., Catlin, D.H., 2018a. Application of Bayesian robust design model to assess the impacts of a hurricane on shorebird demography. Ecosphere 9, e02334.

Gibson, D., Chaplin, M.K., Hunt, K.L., Friedrich, M.J., Weithman, C.E., Addison, L.M., Cavalieri, V., Coleman, S., Cuthbert, F.J., Fraser, J.D., Golder, W., Hoffman, D., Karpanty, S.M., Van Zoeren, A., Catlin, D.H., 2018b. Impacts of anthropogenic disturbance on body condition, survival, and site fidelity of nonbreeding piping plovers. Condor 120, 566–580.

Gibson, D., Hornsby, A.D., Brown, M.B., Cohen, J.B., Dinan, L.R., Fraser, J.D., Friedrich, M.J., Gratto-Trevor, C.L., Hunt, K.L., Jeffery, M., et al., 2019. Migratory shorebird adheres to Bergmann's rule by responding to environmental conditions through the annual lifecycle. Ecography 42, 1482–1493.

Gill, J.A., Norris, K., Potts, P.M., Gunnarsson, T.G., Atkinson, P.W., Sutherland, W.J., 2001. The buffer effect and large-scale population regulation in migratory birds. Nature 412, 436–438.

Gochfeld, M., Burger, J., 1980. Opportunistic scavenging by shorebirds: feeding behavior and aggression. J. Field Ornithol. 51, 373–375.

Gratto-Trevor, C., Amirault-Langlais, D., Catlin, D., Cuthbert, F., Fraser, J., Maddock, S., Roche, E., Shaffer, F., 2012. Connectivity in piping plovers: do breeding populations have distinct winter distributions? J. Wildl. Manag. 76, 348–355.

Gratto-Trevor, C., Haig, S.M., Miller, M.P., Mullins, T.D., Maddock, S., Roche, E., Moore, P., 2016. Breeding sites and winter site fidelity of piping plovers wintering in the Bahamas, a previously unknown major wintering area. J. Field Ornithol. 87, 29–41.

Grosbois, V., Harris, M.P., Anker-Nilssen, T., McCleery, R., Shaw, D., Morgan, B.J., Gimenez, O., 2009. Modeling survival at multi-population scales using mark–recapture data. Ecology 90, 2922–2932.

Haig, S.M., Oring, L.W., 1988. Distribution and dispersal in the piping plover. Auk 105, 630–638.

Haig, S.M., Mehlman, D.W., Oring, L.W., 1998. Avian movements and wetland connectivity in landscape conservation. Conserv. Biol. 12, 749–758.

Haig, S.M., Ferland, C.L., Cuthbert, F.J., Dingledine, J., Goossen, J.P., Hecht, A., McPhillips, N., 2005. A complete species census and evidence for regional declines in piping plovers. J. Wildl. Manag. 69, 160–173.

Harrison, X.A., Blount, J.D., Inger, R., Norris, D.R., Bearhop, S., 2011. Carry-over effects as drivers of fitness differences in animals. J. Anim. Ecol. 80, 4–18.

Henkel, J.R., Sigel, B.J., Taylor, C.M., 2012. Large-scale impacts of the Deepwater Horizon oil spill: can local disturbance affect distant ecosystems through migratory shorebirds? Bioscience 62, 676–685.

Henle, K., Gruber, B., 2018. Performance of multistate mark–recapture models for temporary emigration in the presence of survival costs. Methods Ecol. Evol. 9, 657–667.

Hostetler, J.A., Hallworth, M.T., 2021. MigConnectivity: Estimate Migratory Connectivity for Migratory Animals. R package version 0.4.0.

IPCC, 2019. In: Pörtner, H., Roberts, D., Masson-Delmotte, V., Zhai, P., Tignor, M., Poloczanska, E., Mintenbeck, K., Alegría, A., Nicolai, M., Okem, A., Petzold, J., Rama, B., Weyer, N. (Eds.), IPCC Special Report on the Ocean and Cryosphere in a Changing Climate. In press.

Iwamura, T., Fuller, R.A., Possingham, H.P., 2014. Optimal management of a multispecies shorebird flyway under sea-level rise. Conserv. Biol. 28, 1710–1720.

Jorgensen, J.G., Brown, M.B., Tyre, A.J., 2012. Channel width and least tern and piping plover nesting incidence on the lower Platte river, Nebraska. Gt. Plains Res. 22, 59–67.

Kellner, K., 2019. jagsUI: a wrapper around "rjags" to streamline "JAGS" analyses. https://CRAN.R-project.org/package=jagsUI.

Kendall, W.L., Nichols, J.D., 2002. Estimating state-transition probabilities for unobservable states using capture–recapture/resighting data. Ecology 83, 3276–3284.

Kery, M., Schaub, M., 2011. Bayesian population analysis using WinBUGS: a hierarchical perspective. Academic Press, Waltham, MA, USA.

Kery, M., Madsen, J., Lebreton, J.D., 2006. Survival of Svalbard pink-footed geese *Anser brachyrhynchus* in relation to winter climate, density and land-use. J. Anim. Ecol. 75, 1172–1181.

Koleček, J., Reif, J., Šálek, M., Hanzelka, J., Sottas, C., Kubelka, V., 2021. Global population trends in shorebirds: migratory behaviour makes species at risk. Sci. Nat. 108, 1–8.

Kvitek, R., Bretz, C., 2005. Shorebird foraging behavior, diet, and abundance vary with harmful algal bloom toxin concentrations in invertebrate prey. Mar. Ecol. Prog. Ser. 293, 303–309.

Landsberg, J., 2002. The effects of harmful algal blooms on aquatic organisms. Rev. Fish. Sci. 10, 113–390.

Landsberg, J., Flewelling, L., Naar, J., 2009. *Karenia brevis* red tides, brevetoxins in the food web, and impacts on natural resources: decadal advancements. Harmful Algae 8, 598–607.

Lebreton, J.-D., Burnham, K.P., Clobert, J., Anderson, D.R., 1992. Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. Ecol. Monogr. 62, 67–118.

Lebreton, J.-D., Nichols, J.D., Barker, R.J., Pradel, R., Spendelow, J.A., 2009. Modeling individual animal histories with multistate capture–recapture models. Adv. Ecol. Res. 41, 87–173.

Ledee, O.E., Arnold, T.W., Roche, E.A., Cuthbert, F.J., 2010. Use of breeding and nonbreeding encounters to estimate survival and breeding-site fidelity of the piping plover at the Great Lakes. Ornithol. Appl. 112, 637–643.

Leighton, F.A., 1993. The toxicity of petroleum oils to birds. Environ. Rev. 1, 92–103.

Maggini, I., Kennedy, L.V., Macmillan, A., Elliot, K.H., Dean, K., Guglielmo, C.G., 2017. Light oiling of feathers increases flight energy expenditure in a migratory shorebird. J. Exp. Biol. 220, 2372–2379.

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

Marsh, C.P., Wilkinson, P.M., 1991. The impact of hurricane Hugo on coastal bird populations. J. Coast. Res. SI 8, 327–334.

Martin, T.G., Chadès, I., Arcese, P., Marra, P.P., Possingham, H.P., Norris, D.R., 2007. Optimal conservation of migratory species. PloS One 2, e751.

McClintock, B.T., Langrock, R., Gimenez, O., Cam, E., Borchers, D.L., Glennie, R., Patterson, T.A., 2020. Uncovering ecological state dynamics with hidden markov models. Ecol. Lett. 23, 1878–1903.

McKinnon, E.A., Love, O.P., 2018. Ten years tracking the migrations of small landbirds: lessons learned in the golden age of bio-logging. Auk Ornithol. Adv. 135, 834–856.

Morrison, R., Davidson, N.C., Wilson, J.R., 2007. Survival of the fattest: body stores on migration and survival in red knots *Calidris canutus islandica*. J. Avian Biol. 38, 479–487.

NOAA National Centers for Environmental Information, 2014. Physical and biological data collected along the Texas, Louisiana, Mississippi, Alabama, and Florida Gulf coasts in the Gulf of Mexico as part of the Harmful Algal BloomS Observing System from 1953-08-19 to 2020-03-09 (NCEI Accession 0120767). NOAA National Centers for Environmental Information. Dataset. https://accession.nodc.noaa.gov/0120767.

Northrup, J.M., Gerber, B.D., 2018. A comment on priors for Bayesian occupancy models. PloS One 13, e0192819.

Patrick, C., Yeager, L., Armitage, A., Carvallo, F., Congdon, V., Dunton, K., Fisher, M., Hardison, A., Hogan, J., Hosen, J., et al., 2020. A system level analysis of coastal ecosystem responses to hurricane impacts. Estuar. Coasts 43, 943–959.

Pierce, R.H., Henry, M.S., 2008. Harmful algal toxins of the Florida red tide (Karenia brevis): natural chemical stressors in South Florida coastal ecosystems. Ecotoxicology 17, 623–631.

Plummer, M., 2003. JAGS: a program for analysis of Bayesian graphical models using Gibbs sampling. In: Proc. 3rd Int. Workshop Distrib. Stat. Comput. 124, 1–10. Vienna, Austria.

Raynor, E.J., Pierce, A.R., Owen, T.M., Leumas, C.M., Rohwer, F.C., 2013. Short-term demographic responses of a coastal waterbird community after two major hurricanes. Waterbirds 36, 88–93.

Riecke, T.V., Sedinger, B.S., Williams, P.J., Leach, A.G., Sedinger, J.S., 2019. Estimating correlations among demographic parameters in population models. Ecol. Evol. 9, 13521–13531.

Robinson, S.G., Gibson, D., Riecke, T.V., Fraser, J.D., Bellman, H.A., DeRose-Wilson, A., Karpanty, S.M., Walker, K.M., Catlin, D.H., 2020a. Piping plover population increase after hurricane Sandy mediated by immigration and reproductive output. Condor 122, duaa041.

Robinson, R.A., Meier, C.M., Witvliet, W., Kéry, M., Schaub, M., 2020b. Survival varies seasonally in a migratory bird: linkages between breeding and non-breeding periods. J. Anim. Ecol. 89, 2111–2121.

Roche, E.A., Cohen, J.B., Catlin, D.H., Amirault-Langlais, D.L., Cuthbert, F.J., Gratto-Trevor, C.L., Felio, J., Fraser, J.D., 2010. Range-wide piping plover survival: correlated patterns and temporal declines. J. Wildl. Manag. 74, 1784–1791.

Rockwell, S.M., Wunderle, J.M., Sillett, T.S., Bocetti, C.I., Ewert, D.N., Currie, D., White, J.D., Marra, P.P., 2017. Seasonal survival estimation for a long-distance migratory bird and the influence of winter precipitation. Oecologia 183, 715–726.

Rosenberg, K.V., Dokter, A.M., Blancher, P.J., Sauer, J.R., Smith, A.C., Smith, P.A., Stanton, J.C., Panjabi, A., Helft, L., Parr, M., et al., 2019. Decline of the North American avifauna. Science 366, 120–124.

Runge, C.A., Watson, J.E., Butchart, S.H., Hanson, J.O., Possingham, H.P., Fuller, R.A., 2015. Protected areas and global conservation of migratory birds. Science 350, 1255–1258.

Rushing, C.S., Hostetler, J.A., Sillett, T.S., Marra, P.P., Rotenberg, J.A., Ryder, T.B., 2017. Spatial and temporal drivers of avian population dynamics across the annual cycle. Ecology 98, 2837–2850.

Saunders, S.P., Arnold, T.W., Roche, E.A., Cuthbert, F.J., 2014. Age-specific survival and recruitment of piping plovers *Charadrius melodus* in the Great Lakes region. J. Avian Biol. 45, 437–449.

Saunders, S.P., Cuthbert, F.J., Zipkin, E.F., 2018. Evaluating population viability and efficacy of conservation management using integrated population models. J. Appl. Ecol. 55, 1380–1392.

Schaub, M., Gimenez, O., Schmidt, B.R., Pradel, R., 2004. Estimating survival and temporary emigration in the multistate capture–recapture framework. Ecology 85, 2107–2113.

Shaffer, F., Laporte, P., 1994. Diet of piping plovers on the Magdalen Islands, Quebec. Wilson Bull. 106, 531–536.

Sherfy, M.H., Anteau, M.J., Shaffer, T.L., Sovada, M.A., Stucker, J.H., 2012. Foraging ecology of least terns and piping plovers nesting on Central Platte River sandpits and sandbars. In: U.S. Geological Survey Open-File Report 2012–1059, 50p.

Shumway, S.E., Allen, S.M., Boersma, P.D., 2003. Marine birds and harmful algal blooms: sporadic victims or under-reported events? Harmful Algae 2, 1–17.

Sidle, J.G., Kirsch, E.M., 1993. Least tern and piping plover nesting at sand pits in Nebraska. Colon. Waterbirds 16, 139–148.

Smith, G.J., 2013. The U.S. Geological Survey Bird Banding Laboratory: An integrated scientific program supporting research and conservation of North American birds. In: U.S. Geological Survey Open-File Report 2013–1238, 332 p.

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

Stucker, J.H., Cuthbert, F.J., Winn, B., Noel, B.L., Maddock, S.B., Leary, P.R., Cordes, J., Wemmer, L.C., 2010. Distribution of non-breeding Great Lakes piping plovers (*Charadrius melodus*) along Atlantic and Gulf of Mexico coastlines: ten years of band sightings. Waterbirds 33, 22–32.

Sullivan, B.L., Wood, C.L., Iliff, M.J., Bonney, R.E., Fink, D., Kelling, S., 2009. eBird: a citizen-based bird observation network in the biological sciences. Biol. Conserv. 142, 2282–2292.

Sutherland, W.J., Alves, J.A., Amano, T., Chang, C.H., Davidson, N.C., Max Finlayson, C., Gill, J.A., Gill Jr., R.E., González, P.M., Gunnarsson, T.G., et al., 2012. A horizon scanning assessment of current and potential future threats to migratory shorebirds. Ibis 154, 663–679.

Swift, R.J., Anteau, M.J., Ring, M.M., Toy, D.L., Sherfy, M.H., 2020. Low renesting propensity and reproductive success make renesting unproductive for the threatened piping plover (*Charadrius melodus*). Condor 122, 1–18.

Swift, R.J., Anteau, M.J., Ellis, K.S., Ring, M.M., Sherfy, M.H., Toy, D.L., Koons, D.N., 2021. Spatial variation in population dynamics of northern Great Plains piping plovers. In: U.S. Geological Survey Open-File Report 2020-1152, 211p.

Team, R.Core, 2019. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/.

Trice, T., Landsea, C., 2020. HURDAT: Hurricane Re-Analysis Project. https://CRAN. R-project.org/package=HURDAT.

Tuma, M.E., 2020. Survival, site fidelity, and movement of two migratory shorebirds in the southeastern U.S. University of Florida. M.S. Thesis.

U.S. Fish and Wildlife Service (USFWS), 1985. Determination of endangered and threatened status for the piping plover. USFWS, Washington, D.C., USA.

U.S. Fish and Wildlife Service (USFWS), 2009. Piping plover (*Charadrius melodus*). In: 5-Year Review: Summary and Evaluation. Hadley, Massachusetts, USA.

van Deventer, M., Atwood, K., Vargo, G.A., Flewelling, L.J., Landsberg, J.H., Naar, J.P., Stanek, D., 2012. *Karenia brevis* red tides and brevetoxin-contaminated fish: a high risk factor for Florida's scavenging shorebirds? Bot. Mar. 55, 31–37.

Warnock, N., Jennings, S., Kelly, J.P., Condeso, T.E., Lumpkin, D., 2021. Declining wintering shorebird populations at a temperate estuary in California: a 30-year perspective. Ornithol. Appl. duaaa060.

Webster, M.S., Marra, P.P., Haig, S.M., Bensch, S., Holmes, R.T., 2002. Links between worlds: unraveling migratory connectivity. Trends Ecol. Evol. 17, 76–83.