

Piping Plover (*Charadrius melodus*) demography, behavior, and movement on the Outer Banks of North Carolina

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Thesis submitted to the faculty of the Virginia Polytechnic Institute and State University in partial fulfillment of the requirements for the degree of

Master of Science
in
Wildlife Conservation

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March 21, 2019

Blacksburg, Virginia

Keywords: disturbance, habitat, management, migration, population dynamics, reproductive output, stopover, survival

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ABSTRACT (ACADEMIC)

The Piping Plover (*Charadrius melodus*) is an imperiled shorebird that inhabits sandy beaches along the North American Atlantic Coast. The species' decline has been attributed to habitat loss, disturbance, and predation throughout its range, although most conservation efforts have focused on increasing reproductive output during the breeding season. On the coast of North Carolina, Piping Plovers breed in areas with large amounts of recreational and tourism use. Beach recreation is known to reduce nest success, chick survival, and potentially fitness in other parts of the species' range. To reduce potential negative effects from human activities on breeding Piping Plovers, managers close areas to pedestrian and vehicle access using exclusion buffers delineated by symbolic fencing. However, the reproductive success and population size of Piping Plovers in parts of North Carolina has not appeared to increase as a result of these management strategies, despite the importance of the park and its protections to these birds on their southward migration in the fall.

To understand how disturbance and attempts to mitigate it affected plover demography, we examined Piping Plover population dynamics, brood movement, and migration in North Carolina from 2015–2017. We monitored 46 nests and 19 broods, and we used a logistic exposure nest survival model and Cormack-Jolly-Seber model to estimate reproductive success. We uniquely banded 77 adults and 49 chicks to understand annual

survival and fidelity rates using a live encounter mark-recapture model. During the pre-fledge period, we observed movements of Piping Plover broods, and we gathered information on their environment that may affect their behavior. We recorded 191 brood locations, collected 132 focal chick behavior samples, and 113 potential disturbance environmental samples. We used multiple linear regression to evaluate several hypotheses regarding daily and hourly brood movement rates. We also conducted 22 migratory surveys after the breeding season in 2016 at an area in Cape Hatteras National Seashore thought to be used by large numbers of south-bound migrating Piping Plovers. We used integrated Jolly-Seber and binomial count models on resighting and count data to estimate stopover superpopulation and stopover duration of migrating birds based on their breeding region of origin.

Annual survival of adults from North Carolina ($\bar{x} = 0.69$, $SE = 0.07$) was not different from another population on Fire Island, New York ($\bar{x} = 0.73$, $SE = 0.04$), but the North Carolina population annually had low reproductive success, primarily due to low rates of chick survival. As a result, the North Carolina population was predicted to decline during the study period ($\lambda < 1$ each year). Historically this population has not met the estimated rate of reproductive output needed for a stationary population 1.07 chicks per pair, $SE = 0.69$); therefore, it is likely the population is sustained by immigration from an unknown source. Daily ($\bar{x} = 71.5\text{m}/24\text{hr}$) and hourly ($\bar{x} = 183.3\text{m}/\text{hr}$) brood movements each had considerable variation (Daily: $SD = 70.6$, range = 0.0–327.2m; Hourly: $SD = 262.3$, range = 0.2–1450.9m). Chicks did not appear to move in response to the environmental factors we examined. The rate of brood movement suggests regular daylight monitoring is necessary to adequately protect unfledged broods from anthropogenic

disturbance under current management methods. We found that 569 Piping Plovers (95% CI: 502–651), nearly 15% of the estimated Atlantic Coast population, stopped at a single area in Cape Hatteras National Seashore, North Carolina during fall migration. Birds stayed an average 4–7 weeks, depending on the breeding region from which they migrated, and they primarily used a relatively new protected area. These findings suggest that North Carolina is an important area for Piping Plover ecology during multiple stages of their annual cycle.

ABSTRACT (PUBLIC)

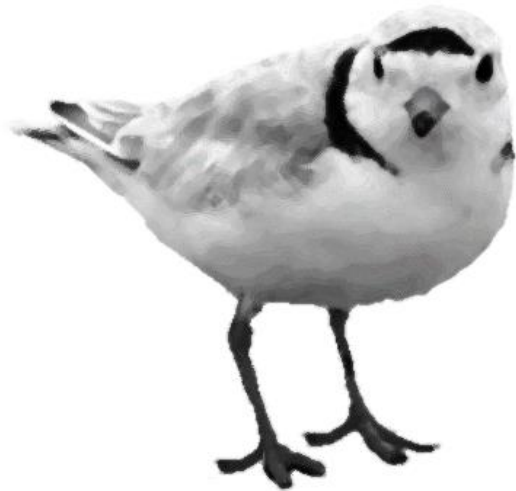
A federally threatened species, the Piping Plover (*Charadrius melodus*) lives on sandy beaches along the North American Atlantic Coast. On the coast of North Carolina, Piping Plovers breed in areas with large amounts of recreational and tourism use. To reduce potential negative effects on breeding Piping Plovers from human activities, land managers close areas to pedestrian and vehicle access. However, the plover population there has not appeared to grow as a result of these management strategies, but large numbers of migrant Piping Plovers have capitalized on this management. Recent work that hypothesized population dynamics in North Carolina may function differently than other Piping Plover populations, and this study was designed to test that hypothesis.

To understand how disturbance, and attempts to mitigate it, affected plover demography, we studied Piping Plover population dynamics, chick movement, and migration in North Carolina from 2015–2017. We monitored breeding efforts of Piping Plovers and used banding techniques to understand survival of chicks and adults. We

observed behavior and movements of Piping Plover chicks before they fledged and gathered information on habitat they selected and potential risks that may alter their behavior. We also conducted migratory surveys after the breeding season at an area thought to be used by large numbers of Piping Plovers.

Survival of adult plovers from North Carolina was not substantially different from that of plovers from other areas, but the North Carolina population had low reproductive success caused by low chick survival, and we estimated the population was declining. However, historically this population has not had enough breeding success to maintain itself; therefore, it is likely the population relies on plovers that immigrate to North Carolina from elsewhere. Plover brood movement was variable, and did not move in response to several environmental factors. The rate of brood movements we observed suggest regular daylight monitoring is necessary to adequately protect unfledged broods from anthropogenic disturbance and mortality using current management methods. We found that nearly 15% of Atlantic Coast plovers stopped at a single area in Cape Hatteras National Seashore, North Carolina, during fall migration, staying an average 4–7 weeks. These findings suggest that North Carolina is a unique area to Piping Plover ecology during multiple stages of their annual cycle.

This is dedicated to the little birds who have taught me big things.



ACKNOWLEDGEMENTS

I would first like to thank my family for their endless love and support. A very special thanks to my parents, who always encouraged me to do what I love, even if they didn't quite understand it at first. They were always there to lend a helping hand, a listening ear, and gas money when I needed it. To my friends, who made every aspect of this journey more fun, more successful, and more enjoyable. Thank you so much for the congratulations when things went well, the commiseration and encouragement when they did not, and all the many happy hour drinks in between. I could not have done this without you.

Thank you to my committee members, who have been gracious and wonderful mentors throughout these years. A very special thanks to my co-advisors, Dr. Dan Catlin and Dr. Jim Fraser. Dan, thank you for the many hours spent debugging R code with me, being a sounding board, and encouraging me to take a break to ride bikes. Jim, thank you for your steadfast advocacy and "full-ahead" attitude, and for always making time for impromptu office conversations. Thank you to Dr. Sarah Karpanty for your valuable guidance and input that made me think critically about my work, and for supporting me with encouraging words and advice. I am a better scientist thanks to all of you.

This thesis would not have been possible without the support of the Virginia Tech Shorebird Program and its members before and during my time. I would like to thank Hen Bellman, Kayla Davis, Audrey DeRose-Wilson, Don Fraser, Meryl Friedrich, Dan Gibson, Kelsi Hunt, Eunbi Kwon, Shannon Ritter, Sam Robinson, and Sara Ziegler. The support from such a great group of hardworking and intelligent colleagues was more than I could have asked for. Thank you for all your help, including all the snacks and laughs shared in

134 Cheatham Hall. Thank you also to the Department of Fish and Wildlife Conservation for support during project planning and implementation.

I also owe much of this success to those that helped gather data in the field. To Nicole DeFelice, Amy Etherington, and Katie Walker, thank you so much for all the grueling, sandy hours you spent with me in the field watching plovers. Your hard work and dedication in the field was crucial, and made the field seasons run smoothly. Thank you for your enthusiasm, your willingness to wake up hours before dawn, and the gallons of shared coffee. An extra special thank you to Katie, for being an amazing roommate and wonderful friend during and after the field season.

Thank you to our many collaborators and funders. Thank you to Cape Hatteras National Seashore, Pea Island National Wildlife Refuge, and Cape Lookout National Seashore for permission to conduct research on their properties. Thank you to Jon Altman, Kristina Fair, Dave Hallac, Rebecca Harrison, Britta Muiznieks, Stacy Sigler, Brian Van Druten, Tracy Ziegler, and the many NPS and USFWS permanent and seasonal staff that I worked alongside while conducting this research. Thank you also to Sidney Maddock for his collaboration both during and after the field season. This work was funded by The National Park Service at Cape Hatteras National Seashore, and conducted under Virginia Tech IACUC permit #16-244.

Lastly, thank you to Cedar. Thank you for your patience during long work days and for reminding me of the healing powers of romps through the woods.

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ATTRIBUTIONS

The following summarizes the contributions made by my coauthors to these manuscripts.

Chapter 1: Growth of Two Atlantic Coast Piping Plover Populations

Samantha Robinson (Department of Fish and Wildlife Conservation, Virginia Tech) collected the data, provided analytical support, and substantially edited the manuscript. Kelsi Hunt (Department of Fish and Wildlife Conservation, Virginia Tech) provided analytical support and edited the manuscript. Jon Altman (National Park Service, Cape Lookout National Seashore), Henrietta Bellman (Department of Fish and Wildlife Conservation, Virginia Tech), Audrey DeRose-Wilson (Delaware Division of Fish and Wildlife), and Katie Walker (Department of Fish and Wildlife Conservation, Virginia Tech) helped collect the data and provided edits to the manuscript. James Fraser (Department of Fish and Wildlife Conservation, Virginia Tech) secured funding, provided support, and substantially edited the manuscript. Sarah Karpanty (Department of Fish and Wildlife Conservation, Virginia Tech) provided support and substantially edited the manuscript. Daniel Catlin (Department of Fish and Wildlife Conservation, Virginia Tech) secured funding, provided analytical support, and substantially edited the manuscript.

Chapter 2: Piping Plover Brood Movement Rates and Their Relationship to Current Management Practices in Parts of North Carolina

James Fraser (Department of Fish and Wildlife Conservation, Virginia Tech) secured funding, contributed to study design, and substantially edited the manuscript. Sarah Karpanty (Department of Fish and Wildlife Conservation, Virginia Tech) substantially

edited the manuscript and contributed to study design. Daniel Catlin (Department of Fish and Wildlife Conservation, Virginia Tech) secured funding, contributed to study design, provided analytical support, and substantially edited the manuscript.

Chapter 3: Discovery of an Important Stopover Location for Migratory Piping Plovers (*Charadrius melodus*) on South Point, Ocracoke Island, North Carolina, USA

Daniel Gibson (Department of Fish and Wildlife Conservation, Virginia Tech) provided analytical support and substantially edited the manuscript. Katie Walker (Department of Fish and Wildlife Conservation, Virginia Tech) helped in data collection and edited the manuscript. Sidney Maddock (Buxton, NC) helped collect data and edited the manuscript. James Fraser (Department of Fish and Wildlife Conservation, Virginia Tech) secured funding and provided substantial edits to the manuscript. Daniel Catlin (Department of Fish and Wildlife Conservation, Virginia Tech) secured funding, provided analytical support, and provided substantial edits to the manuscript. Sarah Karpanty (Department of Fish and Wildlife Conservation, Virginia Tech) provided support for the study and substantially edited the manuscript. This work was previously published in *Waterbirds*, and is used here with permission (Appendix B).

INTRODUCTION

The Piping Plover (*Charadrius melodus*; hereafter, ‘plover’) is a small shorebird found in North America. Plovers have three distinct breeding populations: the Great Plains and Atlantic Coast populations, listed as Threatened, and the Great Lakes population, listed as Endangered under the U.S. Endangered Species Act (U.S. Fish and Wildlife Service 1985). Breeding Atlantic Coast plovers are found from Newfoundland, Canada to North Carolina, USA from April–August (Elliott-Smith and Haig 2004). Male plovers arrive on the breeding grounds to establish nesting territories and attract females by performing acrobatic aerial flights and calls (Cairns 1982). A nest is a shallow scrape in bare sand or in shellbeds in areas with little or no vegetation, in which females lay a full clutch of four eggs (Cairns 1982). Both adults incubate the eggs after clutch completion for approximately four weeks (Elliott-Smith and Haig 2004).

Plover chicks are precocial, mobile within hours after hatch, and they are led by parents to foraging areas (Cairns 1982, Goldin and Regosin 1998). Broods prefer foraging areas that are moist or saturated sand and mud habitats, such as ephemeral pools, pondshores, or bay shores (Loefering and Fraser 1995, Goldin and Regosin 1998, Elias et al. 2000, Cohen et al. 2009). These areas typically provide higher invertebrate abundance and diversity for foraging broods compared to many other habitats found in coastal ecosystems (e.g., ocean intertidal zone), and use of these habitats has been linked to higher chick survival (Loefering and Fraser 1995, Elias et al. 2000, Cohen et al. 2009, DeRose-Wilson et al. 2018). Chicks fledge 25–35 days after hatch, with heavier chicks typically fledging earlier than lighter chicks (Catlin et al. 2014). Migration starts in early July and may last into November (Elliott-Smith and Haig 2004). Plover migration ecology and

behavior is little studied, although there is evidence that plovers will congregate in flocks, with some of the largest recorded occurring in North Carolina (McConnaughey et al. 1990, Elliott-Smith and Haig 2004).

The North Carolina coast is a popular tourist destination, with approximately 2 million annual visitors to Cape Hatteras National Seashore (CAHA) in the past decade (National Park Service 2017). Human recreation can have negative impacts on Piping Plover adults and chicks (Flemming et al. 1988, Burger 1994, Melvin et al. 1994, DeRose-Wilson et al. 2018) and increasing human visitation to CAHA was thought to pose a threat to plovers and other species that nest there. In 2007, Defenders of Wildlife and the National Audubon Society filed a lawsuit against the National Park Service (NPS) and the U.S. Fish and Wildlife Service (USFWS), which alleged inadequate resource protection in relation to off-road vehicles (ORVs) at CAHA (National Park Service 2012). In 2008, the Consent Decree — an agreement between the defendants, plaintiffs, and interveners in the 2007 lawsuit — established interim restrictions on ORVs (Defenders of Wildlife et al. v. National Park Service et al., [Case No. 2:07-CV-45-BO, U.S. District Court, Eastern District of North Carolina, Northern Division]). In 2012, the final ORV Management Plan (ORVMP) was implemented at CAHA (National Park Service 2012). The ORVMP designated seasonal and year-round ORV routes, and it established exclusion buffers for ORVs and pedestrians around breeding plovers and other species of concern that use the seashore in an attempt to reduce the impact of anthropogenic disturbance during the breeding season.

Since the implementation of the ORVMP, reproductive output of plovers at CAHA has remained below the Revised Recovery Plan goal of 1.5 fledged chicks per pair (U.S. Fish and Wildlife Service 1996, Schweitzer 2017). Long term productivity state-wide in

North Carolina is well under this level (mean = 0.52 chicks per pair, $n = 29$ years), yet there has been growth in the estimated population in some years (Schweitzer 2017). These years of increase suggest that the North Carolina population may be driven by other factors in addition to reproductive output. Previous work by Hecht and Melvin (2009) estimated that the Southern Recovery Unit (Delaware, Maryland, Virginia, and North Carolina) may require a lower rate of reproductive output to maintain a stationary population than other Atlantic Coast populations, perhaps due to higher survival of individuals from the Southern Recovery Unit.

Chapter 1 of this thesis addresses the estimated reproductive rate needed for stationarity in North Carolina compared to a disconnected breeding population on Fire Island, New York. Specifically, we investigated several demographic rates for both populations: reproductive output (nesting success and chick survival), survival, and site fidelity. We estimated the reproductive output needed for a stationary population, and we estimated annual population growth for each population.

Management of Piping Plover broods at CAHA under the ORVMP has focused on providing areas around broods that are free from anthropogenic disturbance using exclusion buffers. These buffers are dynamic, in that closed areas are modified to follow brood movements, and they are in place until broods fledge. In Chapter 2, we focus on brood movement patterns and how they pertain to current management strategies. We estimate daily and hourly brood movement rates with respect to foraging opportunities, predation risks and other disturbances, brood behavior, and age. Predictable patterns of brood movement may be used to improve management strategies (i.e., exclusion buffers) designed to reduce the negative effect of human disturbance on plover chicks.

In addition to being the southern-most breeding plover population, North Carolina also hosts plovers throughout the year (Cohen et al. 2008, Elliott-Smith et al. 2015). Anecdotal evidence suggests that CAHA and other areas in North Carolina host large numbers of plovers during migration (Elliott-Smith and Haig 2004), but the number of birds that use the North Carolina during migration has not previously been quantified beyond occasional surveys or counts (McConnaughey et al. 1990, Elliott-Smith and Haig 2004).

In Chapter 3, we describe an area of CAHA used by migrating plovers. We examined the total passage population during fall migration in 2016 and how that relates to the Atlantic Coast population as a whole. We also estimated stopover duration at this site for previously defined groups of Atlantic Coast plovers. This manuscript represents the first quantitative assessment of an area that may be used by a significant portion of this subspecies during an under-studied stage of its life cycle.

Literature Cited

- Burger, J. (1994). The Effect of Human Disturbance on Foraging Behavior and Habitat Use in Piping Plover (*Charadrius melodus*). *Estuaries* 17:695–701.
- Cairns, W. E. (1982). Biology and Behavior of Breeding Piping Plovers. *The Wilson Bulletin* 94:531–545.
- Catlin, D.H., O. Milenkaya, K.L. Hunt, M.J. Friedrich and J.D. Fraser (2014). Can river management improve the Piping Plover's long-term survival on the Missouri River? *Biological Conservation* 180: 196–205.
- Cohen, J. B., L. M. Houghton, and J. D. Fraser (2009). Nesting Density and Reproductive Success of Piping Plovers in Response to Storm- and Human-Created Habitat Changes. *Wildlife Monographs* 173:1–24.
- Cohen, J. B., S. M. Karpanty, D. H. Catlin, J. D. Fraser, and R. A. Fischer (2008). Winter Ecology of Piping Plovers at Oregon Inlet, North Carolina. *Waterbirds* 31:472–479.
- DeRose-Wilson, A. L., K. L. Hunt, J. D. Monk, D. H. Catlin, S. M. Karpanty, and J. D. Fraser (2018). Piping Plover Chick Survival Negatively Correlated With Beach Recreation. *The Journal of Wildlife Management* 82:1608–1616.
- Elias, S. P., J. D. Fraser, and P. A. Buckley (2000). Piping Plover Brood Foraging Ecology on New York Barrier Islands. *Journal of Wildlife Management* 64:346–354.
- Elliott-Smith, E., M. Bidwell, A. E. Holland, and S. M. Haig (2015). Data from the 2011 International Piping Plover Census: U.S. Geological Survey Data Series 922.

- Elliott-Smith, E., and S. M. Haig (2004). Piping Plover (*Charadrius melodus*). In The Birds of North America online (A. F. Poole, Editor). Cornell Lab of Ornithology, Ithaca, NY, USA. <https://birdsna.org/Species-Account/bna/species/pipplo/>
- Flemming, S. P., R. D. Chiasson, P. C. Smith, P. J. Austin-Smith, and R. P. Bancroft (1988). Piping Plover Status in Nova Scotia Related to Its Reproductive and Behavioral Responses to Human Disturbance. *Journal of Field Ornithology* 59:321–330.
- Goldin, M. R., and J. V Regosin (1998). Chick Behavior, Habitat Use, and Reproductive Success of Piping Plovers at Goosewing Beach, Rhode Island. *Journal of Field Ornithology* 69:228–234.
- Hecht, A., and S. M. Melvin (2009). Population Trends of Atlantic Coast Piping Plovers, 1986–2006. *Waterbirds* 32:64–72.
- Loefering, J. P., and J. D. Fraser (1995). Factors Affecting Piping Plover Chick Survival in Different Brood-rearing Habitats. *Journal of Wildlife Management* 59:646–655.
- Melvin, S.M., A. Hecht and C.R. Griffin (1994). Piping Plover Mortalities Caused by Off-Road Vehicles on Atlantic Coast Beaches. *Wildlife Society Bulletin* 22: 409–414.
- McConnaughey, J. L., J. D. Fraser, S. D. Coutu, and J. P. Loefering (1990). Piping Plover Distribution and Reproductive Success on Cape Lookout National Seashore. Unpublished Report to the National Park Service. 89 pages.

National Park Service (2012). Special Regulations, Areas of the National Park System, Cape Hatteras National Seashore Off-Road Vehicle Management. Final Rule. Federal Register 77:3123–3144.

National Park Service (2017). Cape Hatteras National Seashore Annual Park Recreation Visitation Report. [Online.] Available at <https://irma.nps.gov/Stats/SSRSReports>.

Schweitzer, S. H. (2017). 2017 Breeding Season Report for the Piping Plover in North Carolina. Unpublished Report. North Carolina Wildlife Resource Commission, New Bern, NC.

U.S. Fish and Wildlife Service (1985). Determination of Endangered and Threatened Status for the Piping Plover. Final Rule. Federal Register 50:50726–50734.

U.S. Fish and Wildlife Service (1996). Piping Plover (*Charadrius melodus*), Atlantic Coast Population, Revised Recovery Plan. U.S. Fish and Wildlife Service. Hadley, MA.

CHAPTER 1: GROWTH OF TWO ATLANTIC COAST PIPING PLOVER POPULATIONS

Formatted for submission to *The Condor: Ornithological Applications*

Growth of two Atlantic Coast Piping Plover populations

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ABSTRACT

Species listed under the U.S. Endangered Species Act are required to meet stated recovery goals for delisting. These goals often are developed early in the species' conservation history and may need to be updated or refined as new information becomes available. The Atlantic Coast Piping Plover (*Charadrius melodus*), which was listed as threatened in the U.S. more than 30 years ago, has not met recovery goals through much of

its range. Initial recovery goals included maintaining a reproductive output of 1.5 fledged chicks per pair for 5 years. This goal was based on modelling that assumed equal survival rates for adults throughout the range, but recent studies suggest that demographic rates may vary with latitude. To investigate latitudinal variation, we developed demographic and population growth estimates for two breeding populations of Piping Plovers on Fire Island, New York (Latitude $\sim 40.7^\circ\text{N}$) and on the Outer Banks of North Carolina (Latitude $\sim 35.3^\circ\text{N}$) 2013–2017. Breeding success (nest success and pre-fledge chick survival) varied annually but was lower in North Carolina than New York. Average adult true survival in New York ($\bar{x} = 0.73$, SE = 0.04) was similar to rates reported previously for this species, but average survival in North Carolina was lower ($\bar{x} = 0.69$, SE = 0.07). Annual post-fledging survival for both sites, however, was variable and often higher than had been previously reported for Atlantic Coast Piping Plovers (0.43–0.66 for New York; 0.31 and 1.0 for North Carolina). While the estimated reproductive output needed for a stationary population for both sites was similar (1.10 chicks per pair for New York, 95% CI: 0.83–1.41; 1.07 for North Carolina, 95% CI: 0.67–1.59), only the New York population achieved or exceeded these values during our study. Our findings suggest that understanding the variability of population demographic rates would be helpful in refining recovery goals. Moreover, recovery objectives might be achieved sooner if management strategies target population-specific demographic rates.

Keywords: Demography, breeding success, survival, population dynamics, *Charadrius melodus*, population growth, Atlantic Coast, shorebird

INTRODUCTION

The Endangered Species Act (16 USC 1531 et seq.) requires the U.S. Fish and Wildlife Service (USFWS) to develop and implement recovery plans for listed species (Hoekstra et al. 2002). Mirroring the diversity of imperiled species, recovery plans rarely come in a one-size-fits-all approach (Boersma et al. 2001), but these plans are most effective when their goals are linked to a species' ecology (Boersma et al. 2001, Gerber and Hatch 2002). However, recovery goals based on ecology are only as good as the understanding of the ecology used to set those goals (Gerber and Hatch 2002).

Demographic rates (e.g., survival, fecundity) of imperiled species sometimes are used to predict or explain population changes (Gerber and Hatch 2002). Recovery goals, and subsequent management strategies, may then be designed to achieve increases in some demographic rates, leading to increased population growth (Gerber and Hatch 2002). However, even within a single species, the growth of several populations may vary in sensitivity to changes in the same demographic rate (Sæther and Baake 2000). Populations also may be sustained with unique demographic patterns, where some lower demographic rates may be offset by higher rates of one or more others (Villellas et al. 2015). For example, ecological conditions may limit populations to low rates of fecundity, but be compensated for at the population level by higher rates of individual survival, or vice versa. This variation in demographic rates among populations may be a species' response to a range of ecological conditions that affect parts of the life cycle differently (Sexton et al. 2009).

The pattern of separate demographic strategies was observed in two Horned Lark (*Eremophila alpestris*) subspecies located at different elevation, where the adults of the higher elevation subspecies survived better, yet produced fewer young than their lower elevation

relatives, likely in response to a shorter breeding season (Camfield et al. 2010). Similarly, a difference in demography was detected in two White-tailed Ptarmigan (*Lagopus leucura*) populations with similar growth trajectories. Southern populations had high adult survival rates and low fecundity, but northern populations had lower adult survival coupled with fecundity rates double that of the southern population (Wilson and Martin 2011). However, the breeding season length did not significantly differ between the two ptarmigan populations. In this case, the difference might have been due to differences in higher female investment in reproduction at the northern site (Wilson and Martin 2011). Thus, different demographic strategies may then drive similar population trajectories in a single species.

Consideration of geographically unique demographic rates may allow recovery goals to be tailored to populations, potentially reaching species delisting criteria more quickly, thereby potentially reducing a species' extinction risk. Reevaluation of demographic parameters can determine if alteration of recovery goals based upon new data would benefit the species (Harvey et al. 2002, Scott et al. 2005).

The Atlantic Coast Piping Plover (*Charadrius melodus*; hereafter, "plover") was listed as threatened under the Endangered Species Act in 1986 (U.S. Fish and Wildlife Service 1985). This beach-nesting shorebird breeds in April–August, from North Carolina to Newfoundland, and breeding pairs produce a clutch of up to four eggs from which precocial chicks hatch (Elliot-Smith and Haig 2004). To consider delisting plovers, certain population criteria must be met within four recovery units (U.S. Fish and Wildlife Service 1996). Breeding pair goals vary among recovery units, because of assumed variation in carrying capacity (U.S. Fish and Wildlife Service 1996). A goal of sustained reproductive output needed for delisting, however, is applied to all recovery units. That goal (1.5 fledged chicks

per pair for sustained for five years) was set based on assumptions that survival rates of adults and juveniles were similar across recovery units (0.74 and 0.48, respectively; Melvin and Gibbs 1996), and would therefore require similar rates of recruitment.

Long-term trends of plover population growth have suggested there is latitudinal variation in the reproductive output required for a stationary population, and thus population growth, in each Atlantic Coast recovery unit (Hecht and Melvin 2009). However, variation in population growth remains unexplained, particularly for populations at the northern and southern extremes of the breeding range, suggesting that factors other than productivity may differentially influence population growth in each recovery unit (Hecht and Melvin 2009). Specifically, for plovers in the northern-most recovery unit, populations did not appear to respond to relatively high rates of reproductive output (Hecht and Melvin 2009). Instead, regional population declines were largely driven by low rates of juvenile survival (Calvert et al. 2006). Conversely, there was a weak but significant association between population growth and lower rates of reproductive output in the southern recovery unit (Hecht and Melvin 2009). The mismatch of reproductive output and population growth in the northern and southern populations led Hecht and Melvin (2009) to suggest that growth of these populations may hinge more so on adult and juvenile survival and that survival rates may decline with increasing latitude. This potential variation in population dynamics among recovery units on the Atlantic Coast could mean that growing populations may be achieved with increases in different demographic rates.

Plovers inhabit dynamic ecosystems, and they exhibit demographic responses following anthropogenic and natural habitat creation events (Cohen et al. 2009, Catlin et al. 2015, Hunt et al. 2018), so demographic rates may change through time and differ in

populations that experience habitat alteration. Therefore, an updated analysis of demographic rates needed for a growing population could help evaluate and refine recovery goals specific to each recovery unit. Our objective was to estimate current demographic rates for two latitudinally separated Atlantic Coast breeding populations, provide estimates of reproductive output necessary for stationary populations to assess the potential need for unit-specific estimates and thus management, and finally, to assess annual population growth (λ) for each site.

METHODS

Study Area

The Fire Island, New York study area ('FNS'; 40.6652°N, 73.0614°W; Figure 1) consists of ~27 km of Fire and Westhampton Islands off the south shore of Long Island, NY. The Fire Island study area comprised ocean-front sandy beaches, dunes, overwashes, and a barrier island breach formed by Hurricane Sandy, as well as ephemeral pools and sandy beaches on the Long Island Sound.

The North Carolina study area ('NC'; 35.2240°N, 75.5325°W; Figure 1) consists of ~150km of barrier islands on the North Carolina coast, encompassing Cape Hatteras National Seashore ('CAHA'), Pea Island National Wildlife Refuge ('PEA'), and part of Cape Lookout National Seashore ('CALO'). The North Carolina site comprised ocean-front sandy beaches, dunes, ephemeral pools, and beaches on the Pamlico Sound.

Field Methods

We monitored breeding Piping Plovers at Fire Island from 2013–2017 and in North Carolina from 2015–2017. Monitoring occurred on both study areas from late March to late

August. We searched for nests by walking transects, observing behavior, and visually inspecting potential nesting habitat. After discovery, we attempted to check each nest every 1–3 days until hatch or failure. Adults were trapped while incubating and were banded using either a unique 4-color combination or an alphanumeric flag. We banded all chicks as soon as possible after hatch (range 0–14 days) using the same marking scheme as adults, and we attempted to relocate chicks every 1–3 days for 30 days after hatch, since plovers take an average of 25–35 days to fledge (U.S. Fish and Wildlife Service 1996, Catlin et al. 2013). At Fire Island, we kept a distance away from broods that precluded resighting individual chicks at frequent intervals, so chicks were identified and counted based on attending adults, but at the North Carolina sites we were able to resight individuals at every encounter. Nest and brood monitoring at CALO was conducted primarily by National Park Service staff. We searched for banded birds using spotting scopes throughout the study area and the season, and we received auxiliary resightings throughout the year and throughout the species' range (see detailed description in Catlin et al. 2015).

Analytical Methods

Nest survival. We used a logistic-exposure model (Rotella et al. 2000, Shaffer 2004) to estimate plover nest daily survival rate (DSR) similar to Catlin et al. (2015). We considered nests successful if ≥ 1 egg hatched. We tested the fit of the logistic exposure model with a Hosmer and Lemeshow goodness-of-fit test (Hosmer and Lemeshow 1980) on a global model that included covariates that have previously been shown to influence nest DSR (Catlin et al. 2015, Hunt et al. 2018). However, we were interested in how overall nest success varied annually and between each site as opposed to site-specific nest success, so we used a reduced model with additive and interactive effects of site and year. We extrapolated

estimates of DSR from the annual model to 34 days to estimate the probability that a nest survived from initiation to hatch.

Chick survival. We estimated pre-fledge chick survival using different modeling approaches for each site. We used the Lukacs young survival model (Lukacs et al. 2004) to estimate daily apparent chick survival (φ) to 25 days for Fire Island chicks from 2013–2017. The young survival model relies upon identifying broods based on marked parents and counting the maximum number of young at each occasion (Lukacs et al. 2004). It is likely that we violated the assumption of this model that adoptions are not allowed, as this can occur with plover broods at high densities, but it was a rare occurrence in our study (<5% of broods, S.G.R. personal observation). We used daily, age-specific encounter histories, such that occasion 1 was the count of chicks per brood on day 1 after hatch, with the maximum count of chicks observed on each occasion. We performed model selection first on resight rate (p), with apparent pre-fledge survival set to our most complex model with a quadratic time trend of age interacting with year. We tested resight rate fit with constant, time-varying, linear time trend, and quadratic time trend interacting with annual variation, and ranked the models according with AICc. Using the resight rate structure from the top-ranked model, we then modeled survival using additive and interactive year, linear time, quadratic time structures, and modeled combinations, resulting in 15 models.

At the North Carolina sites, unlike at Fire Island, we were able to resight marked chicks regularly; therefore, we estimated pre-fledge chick survival (φ) under a mark-resight framework using a live-recapture Cormack-Jolly-Seber (CJS) model (Lebreton et al. 1992). We included chicks hatched at CAHA from 2015–2017 and PEA in 2017. We excluded chicks banded at CALO because they were not monitored as frequently as in PEA and

CAHA, and the rate of fledged chicks per pair is generally similar between all sites (Schweitzer 2015, 2016, 2017). We estimated survival rates for 5-day intervals until day 25, since resighting efforts were not daily. We built models with constant, linear time trend, and fully time-varying survival and resight parameters with annual variation, and modeled all combinations of structures, resulting in a candidate set of 16 models.

Adult Survival and Site Fidelity. We estimated true survival of individuals using a mark-resight approach and data from birds banded at each site. In our adult survival analysis, we incorporated all birds banded on the Fire Island site, all adults (≥ 1 year old; AHY) from all North Carolina banding sites (CAHA, CALO, and PEA), and hatch year (< 1 year old; HY) individuals from CAHA and PEA. Since we did not include CALO chicks when estimating pre-fledge chick survival, we excluded HY individuals from CALO to accurately calculate post-fledging survival (see below); however, if they returned in following years, we included them as AHY individuals in subsequent years of the model.

To estimate annual adult survival, we used the Barker (1997) survival model. Estimates of apparent survival for mobile species such as birds may be biased low, as survival can be confounded with permanent emigration from the study site (Barker 1997). Using resighting data from the study area and auxiliary resights from elsewhere, this model allows estimation of true survival (S) by accounting for permanent emigration from the study site ($1-F$, where F is the fidelity rate of individuals to the site). Additional, 'nuisance' parameters include resight rate (p), rate of dead recoveries (r), the resight rate during the supplemental period given that an individual survives that period (R), the probability of being resighted and dying during the supplemental period (R'), and the return probability of emigrated individuals (F').

We performed model selection in a two-step process: first, we allowed survival and fidelity to vary annually by group (age \times year), and we explored structures of nuisance parameters that fit the data, including age, year, and additive and interactive effects of those variables. We fixed both r and F' to 0, as there were no dead recoveries nor return of emigrated individuals in our data, and we assumed no site difference in p , as the habitat (open, sandy beaches) was similar and our survey efforts were frequent at both study areas. Second, we used the nuisance parameter structures from step 1 and built models to estimate annual true survival and fidelity for each age and site combination independently from each other.

We were most interested in possible differences between HY and AHY survival and fidelity for each site and annual variation in those rates. Thus, our simplest survival structure was an interactive annual effect of age. This model was considered our null model because of prior knowledge regarding differences in survival related to age (Cohen and Gratto-Trevor 2011, Catlin et al. 2015). Next, we included an additive effect of year for age-specific annual variation. We then explored nested, site-specific age and year effects in survival. We built fidelity structures for age variation, additive age and site variation, and additive age, site, and annual variation. We then modeled with all combinations of hypothesized survival and fidelity structures using parameter structures from step 1 with the lowest AIC_c values, resulting in 24 models. We then used the median \hat{c} test to estimate and correct for overdispersion across the model set.

Population Growth. We estimated annual site-specific population growth (λ) using annual estimates of adult true survival, nest success, and chick survival from each site. We also estimated the reproductive output (fledged chicks per pair) needed to maintain a

stationary population (assumes that immigration was equal to emigration) as a benchmark, against which observed reproductive output can be compared.

We used estimates of HY survival from the Barker (1997) model and our estimates of pre-fledge survival to compute annual post-fledge survival (survival from fledging until the following year) similar to Catlin et al. (2015) and Hunt et al. (2018) using Equation 2:

$$S_{PF} = \frac{S_{HY}}{\phi_c}$$

- S_{PF} is post-fledge survival.
- S_{HY} is HY survival.
- ϕ_c is pre-fledge apparent survival.

We then used estimates of post-fledge survival to estimate site-specific λ each year. An estimate where $\lambda > 1$ indicates a growing population, where an estimate $\lambda < 1$ indicates a shrinking population. To make comparisons, we used methods similar to previous efforts (Cohen and Gratto-Trevor 2011, Catlin et al. 2015, Hunt et al. 2018) to estimate annual population growth (λ_t) with Equation 3:

$$\lambda_t = S_{AHY} + RPB_t S_{PF} + R(1 - P)B_{t-1} S_{AHY} S_{PF}$$

- S_{AHY} is the true survival for AHY birds.
- S_{PF} is post-fledge survival calculated in Equation 2.
- R is the sex ratio (assumed to be 0.5; Cohen and Gratto-Trevor 2011).

- P is the proportion of returning HY birds that breed (assumed to be 0.68; Cohen and Gratto-Trevor 2011).
- B_t is the reproductive output rate in year t and the previous year (measured in fledged chicks per pair).

To estimate the reproductive output needed for stationarity, we used the same equation, but set $\lambda = 1$ and solved for B . Because post-fledge survival was estimated with small sample sizes, we assumed that the coefficient of variation for post-fledge survival was similar to the coefficient variation of adult survival (Catlin et al. 2015, Hunt et al. 2018). We simulated 100,000 values for S_{AHY} and S_{PF} as performed by Cohen and Gratto-Trevor (2011), Catlin et al. (2015), and Hunt et al. (2018), and for each simulation we calculated a mean value of B and 95% confidence intervals.

General Analytical Methods. We set significance levels to $\alpha = 0.05$. We analyzed nest success using PROC NLMIXED and estimated stationarity and population growth using PROC IML in SAS (SAS Institute, Cary, NC). We analyzed adult survival and North Carolina chick survival using statistical program R (R Core Team 2016) to call program MARK (White and Burnham 1999) using the package '*RMark*' (Laake 2013). We analyzed Fire Island chick survival in program MARK. During model selection, we ranked models within a candidate set according to minimum AICc or QAICc (Burnham and Anderson 2002). If the top model in a set held $\geq 95\%$ of the weight, we chose estimates from the top model, otherwise, we model averaged over the candidate set (Burnham and Anderson 2002), and we used the delta method (Powell 2007) to calculate average values and standard errors from the selected models.

RESULTS

Nest Survival

We monitored 196 nests at the Fire Island site (2013–2017), and 46 nests at the North Carolina site (2015–2017). Our global model fit the data (Hosmer and Lemeshow test, $\chi^2_8 = 10.32$, $P = 0.23$). Nest survival varied between years at each site (Figure 2, Appendix Table 2). The highest annual rate of nest success at North Carolina (0.62, 95% CI: 0.37–0.82) was lower than the highest annual rate of nest success at Fire Island (0.80, 95% CI: 0.63–0.90).

Chick Survival

From 2013–2017 we monitored 455 chicks from 111 broods at Fire Island, and from 2015–2017 we monitored 52 chicks from 18 broods in North Carolina. Pre-fledge chick survival (ϕ) was variable among years at both sites (Figure 3), but on average it was lower for chicks in North Carolina ($\bar{x} = 0.17$, SE = 0.06) than on Fire Island ($\bar{x} = 0.44$, SE = 0.01). The resight rate (p) was high ($\bar{x} = 0.99$, SE < 0.01) in North Carolina for all years during the pre-fledging period, but the resight rate at Fire Island was much more variable during the pre-fledging period (range: 0.58–0.99).

Adult Survival and Site Fidelity

We banded 151 adults (AHY) and 352 chicks (HY) at the Fire Island site and 77 adults and 49 chicks at the North Carolina site. We corrected for estimated overdispersion in the data ($\hat{c} = 1.20$). The first step in our modeling suggested that the most suitable parameter structures were constant, except supplemental period resight rate given survival (R), which varied by age (Appendix Table 4). Therefore, we proceeded with step 2 by

constraining the nuisance parameters in this way (Appendix Table 5). While there was support for differences in fidelity between sites (site variable was contained in half the models with $\geq 1\%$ of the model weight, Appendix Table 5), fidelity estimates for each age group were similar between sites: average AHY fidelity (F) at both sites was high and similar (North Carolina: $\bar{x} = 0.94$, SE = 0.05; Fire Island: $\bar{x} = 0.92$, SE = 0.04). Estimates for HY birds suggested lower fidelity, but were not significantly different from older birds (North Carolina: $\bar{x} = 0.85$, SE = 0.13; Fire Island: $\bar{x} = 0.81$, SE = 0.09; Table 1).

True survival (S) varied by age and year for Fire Island, but there was less evidence for annual variation for North Carolina birds (Figure 4, Appendix Table 6). While average survival estimates between sites were similar, there was strong model support for site-related differences, (i.e., all models with $\geq 1\%$ of the model weight included this difference; Appendix Table 5). Average AHY true survival for Fire Island birds ($\bar{x} = 0.73$, SE = 0.04) was higher than for North Carolina birds ($\bar{x} = 0.69$, SE = 0.07), but this difference was not significant. Average survival for HY birds from Fire Island ($\bar{x} = 0.23$, SE = 0.04) was also higher than HY survival from North Carolina ($\bar{x} = 0.08$, SE = 0.06). Survival for both AHY and HY birds from Fire Island was higher than North Carolina birds of the same age in all years (Figure 4). Post-fledging survival was similar for both sites and generally higher than pre-fledge survival rates (Table 1).

Population Growth

Estimated λ for Fire Island was near to or greater than 1 for four of the five years (Figure 5). North Carolina λ was less than 1 for all years of the study, even when accounting for confidence intervals (Figure 5). The estimated reproductive output needed for

stationarity (population neither growing nor shrinking) at Fire Island was 1.10 fledged chicks per pair (95% CI: 0.83–1.41), similar to that needed in North Carolina (1.07 fledged chicks per pair, 95% CI: 0.67–1.59). The reproductive output at Fire Island exceeded the rate needed for stationarity in three of the five years during the study, and North Carolina reproductive output never achieved the rate needed for stationarity (Table 1).

DISCUSSION

Demographic rates for the Atlantic Coast Piping Plover differed between two populations and through time, but the reproductive output required for stationarity estimated from these data were similar. However, population growth trajectories differed, and only one population had positive growth. Our results suggest that these populations may operate in demographically unique ways, yet appear to require similar rates of reproductive output to achieve growing populations.

Breeding success rates (nest success and pre-fledge chick survival) varied at each site, but the rates for the North Carolina population were generally lower than those at Fire Island. Differences between nest success and chick survival between the sites likely are due to site-specific differences in habitat and predator communities. In 2012, Hurricane Sandy struck Fire Island, creating multiple island breaches and overwash areas and increasing the amount of suitable plover nesting habitat (K. Walker et al. in review). It is possible the habitat created by Hurricane Sandy had a positive effect on nest and chick survival in ways similarly observed following large-scale habitat creation on the Missouri River (Catlin et al. 2015, Hunt et al. 2018). Changes in Fire Island geomorphology from Hurricane Sandy also provided more access to bay-side tidal habitats for foraging (K. Walker et al. in review). Bay-side tidal foraging habitats can provide high prey abundance, which is related to higher

chick foraging rates and higher pre-fledge survival rates (Loefering and Fraser 1995, Elias et al. 2000, Cohen et al. 2009). The habitat created by Hurricane Sandy may have bolstered nest and pre-fledge chick survival at the Fire Island site, but demographic rates before the storm were not available for comparison. In contrast, the North Carolina site has not had a similar habitat-creating event since Hurricane Irene in 2011 (Avila and Cangialosi 2013). Since our study did not begin immediately following Hurricane Irene, as Fire Island monitoring did following Hurricane Sandy, North Carolina breeding success rates likely were not influenced by storm-created habitat.

Predator communities and other disturbance sources likely differ at each site and may limit breeding success. Kwon et al. (2018) found significantly lower daily survival rates of plover nests with nearby ghost crab (*Ocyrode quadrata*) burrows in parts of our North Carolina study site, whereas nest and chick depredation by red foxes (*Vulpes vulpes*) contributes to low plover nest and chick survival on Fire Island in some years (U.S. Fish and Wildlife Service 2014). Cohen et al. (2009) also found that plover chick survival was positively correlated with the number of cats and foxes removed on Westhampton Island, NY (Figure 1). While plover nests at both study areas are protected by predator exclosures (Melvin et al. 1992), the extent of protection from human disturbance by symbolic fencing, (i.e., minimum distance from a nest where a symbolic fence is erected) and the amount of human traffic around nesting areas vary within and between sites. Symbolic fencing also is used in North Carolina to protect plover broods, but this management technique often is not consistent on Fire Island, and chick survival appears to be related to human disturbance on those beaches (DeRose-Wilson et al. 2018). Thus, the external factors that contribute to nest

success and pre-fledge chick survival are variable and likely unique to each of our study sites.

There was model support for annual site differences in adult survival, yet estimates for both sites were not significantly different. Average AHY true survival in Fire Island was similar to previously reported estimates of true survival (0.70 at Westhampton Dunes, NY, Cohen et al. 2006; 0.76 in the Great Lakes, LeDee et al. 2010; 0.76 in the Great Plains, Catlin et al. 2015), and North Carolina estimates from both years were relatively low when compared to previous estimates of true survival (reviewed in Catlin et al. 2015).

Since each site had different annual trends in survival, it is possible that site-dependent factors play an important role in adult plover survival. As different predator communities likely influence nest success and chick survival at each site, those predator threats may influence the breeding adults respectively. American mink (*Neovison vison*) have been observed depredating nesting adults in North Carolina (C.E.W, personal observation), whereas red foxes and Peregrine Falcons (*Falco peregrinus*) may be important predators of adult plovers on Fire Island in some years (U.S. Fish and Wildlife Service 2014; S.G.R, personal observation). In addition, Fire Island plovers migrate farther on average to their wintering grounds than plovers from North Carolina (Gibson et al. in review), suggesting that costs related to migration distance likely do not have a significant effect on adult survival (Hecht and Melvin 2009), but other aspects of migration (e.g., stopover locations and duration; Weithman et al. 2018) may influence survival (McGowan et al. 2011). However, relatively little is known about the ecology of plover migration and its influence on the population.

In contrast to adult survival, post-fledging survival for both sites was higher in some years than the assumed rate of 0.48 used to set recovery goals (U.S. Fish and Wildlife Service 1996) and other survival rates previously reported (see Catlin et al. 2015 for review). Post-fledging estimates from this study were comparable to AHY survival rates in some years. The pattern of significantly lower survival for first-year individuals compared to adults appears common in shorebirds (Colwell 2010), so these high rates of post-fledging survival at both sites are particularly interesting. Hecht and Melvin (2009) suggested that differences in survival with latitude may affect post-fledged birds in particular (i.e., northern fledglings have lower survival than southern ones); however, we did not detect this pattern when comparing these two populations.

High post-fledging survival rates contributed to estimates of the reproductive output needed for stationarity at our sites that were similar to previous estimates for other plover populations (Calvert et al. 2006, Cohen and Gratto-Trevor 2011). However, post-fledging survival rates for North Carolina were estimated using few individuals ($n = 5$), so these estimates may be particularly susceptible to stochastic variation due to the small number of fledglings produced each year (Schweitzer 2017). Thus, population growth in North Carolina may be more susceptible to stochastic variation in post-fledging survival than on Fire Island (Sæther and Baake 2000).

Hecht and Melvin (2009) found that a similar rate of reproductive output (1.01 fledged chicks per pair) would be needed for the New York and New Jersey recovery unit to maintain a stationary population. Their estimate for the southern recovery unit (0.93 fledged chicks per pair) was lower than ours, but it fell within our 95% confidence intervals. Their analysis suggested that demographic factors other than reproductive output may be

relatively more important to population growth in some populations (Melvin and Gibbs 1996, Larson et al. 2000, Hecht and Melvin 2009). Indeed, there has been recent evidence to suggest that population growth for different plover populations operate in unique ways. Plover population growth in Eastern Canada was most sensitive to variation in adult and post-fledge survival (Calvert et al. 2006), but population growth in the Great Lakes was less so (Saunders et al. 2018). Therefore, while populations may achieve growth with similar levels of reproductive output, modest increases in other demographic rates may achieve similar population sizes more quickly. Additionally, estimates by Hecht and Melvin (2009) were calculated at larger population scales, so those estimates may also encompass metapopulation dynamics, if there is significant dispersal that occurs within each recovery unit.

Our estimates of the reproductive output required for stationarity do not directly account for adult immigration at each site. Because of the difficulty of estimating immigration, we assumed that the rate of emigration equals the rate of immigration for adults, and thus neither rate contributes to population growth. It is possible that immigration of adults from other populations may moderate negative population growth that is caused by the effects of low adult survival or productivity (Pulliam 1988). However, observed declines in the North Carolina population during the study (Schweitzer 2017) are similar to our estimated λ . The similarity of our estimates and observed numbers suggests that immigration did not mitigate population losses due to low reproductive output and survival. However, historically, North Carolina has rarely achieved our estimated rate of reproductive output needed for stationarity, yet the population has fluctuated (Schweitzer 2017), suggesting that immigration may play an important role in sustaining the population

in some years. In contrast, positive population growth at Fire Island through the study may be driven by a combination of high reproductive output and immigration (Cohen et al. 2009), as observations of unbanded nesting birds (which we assume are individuals that were not present at our site the previous year based on banding records) increased later in the study (S.G.R, personal observation). Given that plovers commonly colonize newly created habitat (Wilcox 1959, Cohen et al. 2009, Schupp et al. 2013), the population growth at Fire Island may have benefitted from immigrants capitalizing on habitat created by Hurricane Sandy (Walker et al. in review). Continued refinement of population growth estimates may benefit from quantifying immigration effects along with other demographic rates (Schaub and Abadi 2010, Saunders et al. 2018).

Recovery efforts for Atlantic Coast Piping Plovers have focused on increasing reproductive output to increase pair numbers (U.S. Fish and Wildlife Service 1996). However, despite more than three decades of management on the breeding grounds to increase reproductive output (Flemming et al. 1988, Melvin et al. 1992, Burger 1994, Cohen et al. 2016), most recovery units are still below population levels required for delisting (U.S. Fish and Wildlife Service 2017). Unattained reproductive output goals may partially be due to inadequate foraging resources (Loefering and Fraser 1995, Elias et al. 2000, Cohen et al. 2009), but how that same habitat limitation may affect adult plover survival remains unclear, except perhaps in the case of extreme habitat loss (Catlin et al. 2015, Hunt et al. 2018). Limitation of suitable foraging habitat (Wilcox 1959, Cohen et al. 2009, Schupp et al. 2013) may hamper achievement of recovery goal pair counts within each recovery unit by inhibiting immigration and increasing emigration (Cohen et al. 2009, Catlin et al. 2015), but its effect on adult survival is less clear (Catlin et al. unpublished data).

Understanding what is limiting population growth of a migratory species can be difficult, even for one that is as heavily monitored through the breeding season as plovers. Recent research has begun to elucidate factors that affect survival throughout the year, and how these factors may disproportionately affect certain populations (LeDee et al. 2010, Roche et al. 2010, Gratto-Trevor et al. 2012, Gibson et al. 2018). Recovery goals may be obtained sooner if management strategies designed to increase local adult survival are implemented in conjunction with long-standing breeding success strategies and habitat protection, especially if population growth is sensitive to adult and post-fledging survival (Calvert et al. 2006). In addition, continued study to tease out the effects of annual stochasticity from long-term trends (Lebreton et al. 1992) in these populations would help to refine estimates of population growth for plovers.

ACKNOWLEDGMENTS

We thank the National Park Service, the U.S. Fish and Wildlife Service, the U.S. Army Corps of Engineers, Suffolk County Parks, New York State Parks, and the North Carolina Wildlife Resource Commission for permission to work on their property and for support during this study. We thank R. Harrison, M. Havens, B. Muiznieks, S. Papa, S. Sigler, and R. Smith for support of this work. We also thank the many permanent and seasonal staff at our sites that provided communication and other logistical support during this study. We are especially grateful to the members of the Virginia Tech Shorebird Program for their support in the field and office. We are appreciative of the numerous field technicians who helped collect these data, and the many individuals who provided resights of banded birds throughout the year.

Funding statement: Funding for this study was provided by the U.S. Army Corps of Engineers to the U.S. Fish and Wildlife Service under the Fire Island to Moriches Inlet Biological Opinion, the U.S. Fish and Wildlife Service, the National Park Service, and by Virginia Tech.

Ethics statement: This research was conducted under Institutional Animal Care and Use Committee protocol #16-244, U.S. Geological Survey Federal Bird Banding permit #21446, U.S. Fish and Wildlife Service Endangered Species permits #TE-103272-3 and #TE-697823, U.S. National Park Service Scientific Research and Collecting permits CAHA-2015-SCI-0009, CAHA-2016-SCI-0003, CAHA-2017-SCI-0005, CALO-2015-SCI-0002, CALO-2016-SCI-0003, CALO-2017-SCI-0002, FIIS-2013-SCI-0002, FIIS-2015-SCI-0011, FIIS-2016-SCI-0003, FIIS-2017-SCI-0004, North Carolina Wildlife Resource Commission Endangered Species permits #438, Research and Monitoring Special Use permits 2016-006R and 2017-003R, New York State Department of Environmental Conservation Endangered Species permit #314, New York State Office of Parks, Recreation and Historic Preservation permits 15-0700, 16-0393, 17-0755, and permits for Research in Suffolk County Parklands.

Author Contributions: D.H.C., J.D.F., and S.M.K. conceived and designed the study and secured funding. C.E.W., S.G.R., J.A., H.A.B., A.L.D., and K.M.W. conducted fieldwork and collected data. C.E.W., S.G.R., and K.L.H. analyzed the data, and D.H.C. provided substantial analytical support. C.E.W. and S.G.R. wrote the manuscript. D.H.C., J.D.F., K.L.H., and S.M.K. substantially edited the manuscript.

LITERATURE CITED

- Avila, L. A., and J. Cangialosi (2013). Tropical Cyclone Report, Hurricane Irene (AL092011) 21–28 August 2011. U.S. Department of Commerce, National Oceanic and Atmospheric Administration, National Hurricane Center, Miami, Florida.
https://www.nhc.noaa.gov/data/tcr/AL092011_Irene.pdf, accessed 2 February 2018.
- Barker, R. J. (1997). Joint Modeling of Live-Recapture, Tag-Resight, and Tag-Recovery Data. *Biometrics* 53:666–677.
- Boersma, P. D., P. Kareiva, W. F. Fagan, J. A. Clark, and J. M. Hoekstra (2001). How Good Are Endangered Species Recovery Plans? *BioScience* 51:643–649.
- Burger, J. (1994). The Effect of Human Disturbance on Foraging Behavior and Habitat Use in Piping Plover (*Charadrius melodus*). *Estuaries* 17:695–701.
- Burnham, K. P., and D. R. Anderson (2002). *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*. Second Ed. Springer-Verlag, New York, New York, USA.
- Calvert, A. M., D. L. Amirault, F. Shaffer, R. Elliot, A. Hanson, J. McKnight, and P. D. Taylor (2006). Population Assessment of an Endangered Shorebird: the Piping Plover (*Charadrius melodus melodus*) in Eastern Canada. *Avian Conservation and Ecology* 1:1–22.
- Camfield, A. F., S. F. Pearson, and K. Martin (2010). Life history variation between high and low elevation subspecies of horned larks *Eremophila* spp. *Journal of Avian Biology* 41:273–281.
- Catlin, D. H., J. H. Felio, and J. D. Fraser (2013). Effects of water discharge on fledging time, growth, and survival of Piping Plovers on the Missouri River. *Journal of Wildlife Management* 77:525–533.
- Catlin, D. H., J. D. Fraser, and J. H. Felio (2015). Demographic Responses of Piping Plovers to Habitat Creation on the Missouri River. *Wildlife Monographs* 192:1–42.

- Cohen, J. B., J. D. Fraser, and D. H. Catlin (2006). Survival and site fidelity of Piping Plovers on Long Island, New York. *Journal of Field Ornithology* 77:409–417.
- Cohen, J. B., and C. Gratto-Trevor (2011). Survival, site fidelity, and the population dynamics of Piping Plovers in Saskatchewan. *Journal of Field Ornithology* 82:379–394.
- Cohen, J. B., A. Hecht, K. F. Robinson, E. E. Osnas, A. J. Tyre, C. Davis, A. Kocek, B. Maslo, and S. M. Melvin (2016). To exclose nests or not: structured decision making for the conservation of a threatened species. *Ecosphere* 7:1–15.
- Cohen, J. B., L. M. Houghton, and J. D. Fraser (2009). Nesting Density and Reproductive Success of Piping Plovers in Response to Storm- and Human-Created Habitat Changes. *Wildlife Monographs* 173:1–24.
- Colwell, M. A. (2010). *Shorebird Ecology, Conservation, and Management*. University of California Press, Berkeley, California.
- DeRose-Wilson, A. L., K. L. Hunt, J. D. Monk, D. H. Catlin, S. M. Karpanty, and J. D. Fraser (2018). Piping Plover Chick Survival Negatively Correlated with Beach Recreation. *Journal of Wildlife Management* 82:1608–1616.
- Elias, S. P., J. D. Fraser, and P. A. Buckley (2000). Piping Plover Brood Foraging Ecology on New York Barrier Islands. *Journal of Wildlife Management* 64:346–354.
- Elliott-Smith, E., and S. M. Haig (2004). Piping Plover (*Charadrius melodus*). In *The Birds of North America online* (A. F. Poole, Editor). Cornell Lab of Ornithology, Ithaca, NY, USA. <https://birdsna.org/Species-Account/bna/species/pipplo/>
- Flemming, S. P., R. D. Chiasson, P. C. Smith, P. J. Austin-smith, and R. P. Bancroft (1988). Piping Plover Status in Nova Scotia Related to Its Reproductive and Behavioral Responses to Human Disturbance. *Journal of Field Ornithology* 59:321–330.
- Gerber, L. R., and L. T. Hatch (2002). Are we recovering? An evaluation of recovery criteria under the U.S. Endangered Species Act. *Ecological Applications* 12:668–673.

- Gibson, D., H. Hornsby, M. Bomberger Brown, J. Cohen, L. Dinan, J. Fraser, M. Friedrich, C. L. Gratto-Trevor, K. Hunt, M. Jeffery, J. Jorgensen, P. Paton, S. Robinson, J. Rock, M. Stantial, C. Weithman, and D. Catlin. Migratory shorebird adheres to Bergmann's Rules by responding to environmental conditions through the annual lifecycle. *Ecography*. *In review*.
- Gibson, D., M. K. Chaplin, K. L. Hunt, M. J. Friedrich, C. Weithman, L. M. Addison, V. Cavalieri, S. Coleman, F. J. Cuthbert, J. D. Fraser, W. Golder, et al. (2018). Impacts of anthropogenic disturbance on non-breeding body condition, survival, and population growth of a shorebird. *The Condor: Ornithological Applications* 120:566–580.
- Gratto-Trevor, C., D. Amirault-Langlais, D. Catlin, F. Cuthbert, J. Fraser, S. Maddock, E. Roche, and F. Shaffer (2012). Connectivity in Piping Plovers: Do Breeding Populations Have Distinct Winter Distributions? *Journal of Wildlife Management* 76:348–355.
- Harvey, E., J. M. Hoekstra, R. J. O'Connor, and W. F. Fagan (2002). Recovery plan revisions: Progress or due process? *Ecological Applications* 12:682–689.
- Hecht, A., and S. M. Melvin (2009). Population Trends of Atlantic Coast Piping Plovers, 1986–2006. *Waterbirds* 32:64–72.
- Hoekstra, J. M., J. A. Clark, W. F. Fagan, and P. D. Boersma (2002). A Comprehensive Review of Endangered Species Act Recovery Plans. *Ecological Applications* 12:630–640.
- Hosmer, D. W., and S. Lemeshow (1980). Goodness of fit tests for the multiple logistic regression model. *Communications in Statistics- Theory and Methods* 9:1043–1069.
- Hunt, K. L., J. D. Fraser, M. J. Friedrich, S. M. Karpanty, and D. H. Catlin (2018). Demographic response of Piping Plovers suggests that engineered habitat restoration is no match for natural riverine processes. *The Condor: Ornithological Applications* 120:149–165.
- Kwon, E., J. D. Fraser, D. H. Catlin, S. M. Karpanty, C. E. Weithman, and B. Muiznieks (2018). Presence of Ghost Crabs and Piping Plover Nesting Success. *Journal of*

Wildlife Management 82:850–856.

Laake, J. L. (2013). RMark: An R Inference for Analysis of Capture-Recapture Data with MARK. AFSC Processed Report 2013-01, Alaska Fisheries Science Center, NOAA National Marine Fisheries Services, Seattle, WA, USA.

Larson, M. A., M. R. Ryan, and B. G. Root (2000). Piping Plover Survival in the Great Plains: An Updated Analysis. *Journal of Field Ornithology* 71:721–729.

Lebreton, J. D., K. P. Burnham, J. Clobert, and D. R. Anderson (1992). Modeling Survival and Testing Biological Hypotheses Using Marked Animals: A Unified Approach with Case Studies. *Ecological Monographs* 62:67–118.

LeDee, O. E., T. W. Arnold, E. A. Roche, and F. J. Cuthbert (2010). Use of breeding and nonbreeding encounters to estimate survival and breeding-site fidelity of the Piping Plover at the Great Lakes. *Condor* 112:637–643.

Loefering, J. P., and J. D. Fraser (1995). Factors Affecting Piping Plover Chick Survival in Different Brood-Rearing Habitats. *Journal of Wildlife Management* 59:646–655.

Lukacs, P. M., V. J. Dreitz, F. L. Knopf, and K. P. Burnham (2004). Estimating survival probabilities of unmarked dependent young when detection is imperfect. *Condor* 106:926–931.

McGowan, C. P., J. E. Hines, J. D. Nichols, J. E. Lyons, D. R. Smith, K. S. Kalasz, L. J. Niles, A. D. Dey, N. A. Clark, P. W. Atkinson, C. D. T. Minton, and W. Kendall (2011). Demographic consequences of migratory stopover: linking red knot survival to horseshoe crab spawning abundance. *Ecosphere* 2:1–22.

Melvin, S. M., L. H. MacIvor, and C. R. Griffin (1992). Predator exclosures: A technique to reduce predation at Piping Plover nests. *Wildlife Society Bulletin* 20:143–148.

Melvin, S. M., and J. P. Gibbs (1996). Viability analysis for the Atlantic coast population of Piping Plovers. Pages 175–186 in *Piping Plover (*Charadrius melodus*)*, Atlantic coast population, revised recovery plan. U.S. Fish and Wildlife Service, Hadley,

Massachusetts.

- Powell, L. (2007). Approximating variance of demographic parameters using the delta method: A reference for avian biologists. *Condor* 109:949–954.
- Pulliam, H. R. (1988). Sources, Sinks, and Population Regulation. *The American Naturalist* 132:652–661.
- R Core Team (2016). R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org>.
- Roche, E. A., J. B. Cohen, D. H. Catlin, D. L. Amirault-Langlais, F. J. Cuthbert, C. L. Gratto-Trevor, J. Felio, and J. D. Fraser (2010). Range-Wide Piping Plover Survival: Correlated Patterns and Temporal Declines. *Journal of Wildlife Management* 74:1784–1791.
- Rotella, J. J., M. L. Taper, and A. J. Hansen (2000). Correcting nesting-success estimates for observer effects: maximum-likelihood estimates of daily survival rates with reduced bias. *Auk* 117:92–109.
- Sæther, B.E., and Ø. Baake (2000). Avian Life History Variation and Contribution of Demographic Traits to the Population Growth Rate. *Ecology* 81:642–653.
- Saunders, S. P., F. J. Cuthbert, and E. F. Zipkin (2018). Evaluating population viability and efficacy of conservation management using integrated population models. *Journal of Applied Ecology* 00:1–13.
- Schaub, M., and F. Abadi (2010). Integrated population models: a novel analysis framework for deeper insights into population dynamics. *Journal of Ornithology* 152:1–11.
- Schupp, C. A., N. T. Winn, T. L. Pearl, J. P. Kumer, T. J. B. Carruthers, and C. S. Zimmerman (2013). Restoration of overwash processes creates Piping Plover (*Charadrius melodus*) habitat on a barrier island (Assateague Island, Maryland). *Estuarine, Coastal and Shelf Science* 116:11–20.

- Schweitzer, S. H. (2015). 2015 Breeding Season Report for the Piping Plover in North Carolina. North Carolina Wildlife Resource Commission. New Bern, North Carolina.
- Schweitzer, S. H. (2016). 2016 Breeding Season Report for the Piping Plover in North Carolina. North Carolina Wildlife Resource Commission. New Bern, North Carolina.
- Schweitzer, S. H. (2017). 2017 Breeding Season Report for the Piping Plover in North Carolina. North Carolina Wildlife Resource Commission. New Bern, North Carolina.
- Scott, J. M., D. D. Goble, J. A. Wiens, D. S. Wilcove, M. Bean, and T. Male (2005). Recovery of imperiled species under the Endangered Species Act: the need for a new approach. *Frontiers in Ecology and the Environment* 3:383–389.
- Sexton, J. P., P. J. McIntyre, A. L. Angert, and K. J. Rice (2009). Evolution and Ecology of Species Range Limits. *Annual Review of Ecology, Evolution, and Systematics* 40:415–436.
- Shaffer, T. L. (2004). A unified approach to analyzing nest success. *Auk* 121:526–540.
- U.S. Fish and Wildlife Service (1985). Determination of endangered and threatened status for the Piping Plover. *Federal Register* 50: 50726-50734.
- U.S. Fish and Wildlife Service (1996). Piping Plover (*Charadrius melodus*), Atlantic Coast Population, Revised Recovery Plan. U.S. Fish and Wildlife Service. Hadley, Massachusetts.
- U.S. Fish and Wildlife Service (2014). Biological Opinion and Conference Opinion, Fire Island Inlet to Moriches Inlet, Fire Island Stabilization Project. U.S. Fish and Wildlife Service. Suffolk County, NY.
- U.S. Fish and Wildlife Service (2017). Abundance and productivity estimates - 2016 update: Atlantic Coast Piping Plover population. U.S. Fish and Wildlife Service. Hadley, Massachusetts.

- Villellas, J., D. F. Doak, M. B. García, and W. F. Morris (2015). Demographic compensation among populations: What is it, how does it arise and what are its implications? *Ecology Letters* 18:1139–1152.
- Walker, K.M., J. D. Fraser, D. H. Catlin, S. J. Ritter, S. G. Robinson, H. A. Bellman, A. DeRose-Wilson, S. M. Karpanty, and S. T. Papa. Hurricane Sandy and Engineered Human Response Created Habitat for a Threatened Species. *Ecosphere*. *In review*.
- Weithman, C. E., D. Gibson, K. M. Walker, S. B. Maddock, J. D. Fraser, S. M. Karpanty, and D. H. Catlin (2018). Discovery of an Important Stopover Location for Migratory Piping Plovers (*Charadrius melodus*) on South Point, Ocracoke Island, North Carolina, USA. *Waterbirds* 41:56–62.
- White, G. C., and K. P. Burnham (1999). Program MARK: survival estimation from populations of marked animals. *Bird Study* 46:S120–S139.
- Wilcox, L. R. (1959). A Twenty Year Banding Study of the Piping Plover. *Auk* 76:129–152.
- Wilson, S., and K. Martin (2011). Life-history and demographic variation in an alpine specialist at the latitudinal extremes of the range. *Population Ecology* 53:459–471.

Table 1. Annual estimates of select demographic rates for Piping Plovers on Fire Island, NY (FNS) 2013–2017 and in North Carolina (NC) 2015–2017. Groups were hatch-year (HY) or after-hatch-year (AHY) birds. Values presented are the mean \pm 1 SE.

Site	Year	Post-fledge survival ^a	HY Fidelity ^b	AHY Fidelity ^b	Reproductive Output (chicks per pair) ^c
	2013	0.45 \pm 0.12	0.81 \pm 0.09	0.92 \pm 0.04	0.49 \pm 0.17
	2014	0.43 \pm 0.09	0.81 \pm 0.09	0.91 \pm 0.04	1.39 \pm 0.23
FNS	2015	0.66 \pm 0.07	0.81 \pm 0.09	0.92 \pm 0.04	0.59 \pm 0.14
	2016	0.61 \pm 0.06	0.81 \pm 0.09	0.92 \pm 0.04	1.96 \pm 0.19
	2017 ^d	—	—	—	1.44 \pm 0.14
	2015	1.00 \pm 0.00 ^e	0.85 \pm 0.13	0.94 \pm 0.05	0.20 \pm 0.18
NC	2016	0.31 \pm 0.11	0.85 \pm 0.13	0.94 \pm 0.05	0.55 \pm 0.28
	2017 ^d	—	—	—	0.29 \pm 0.20

^a Post-fledge survival = HY true survival/pre-fledge apparent survival (Equation 2).

^b Fidelity for HY and AHY plovers was estimated using the Barker (1997) model.

^c Reproductive output was estimated using similar methods as Cohen and Gratto-Trevor (2006), Catlin et al. (2015), and Hunt et al. (2018).

^d Post-fledging survival and fidelity rates for HY and AHY plovers were not estimable for the final year of the study.

^e Post-fledge survival in 2015 for NC plovers was set to 1.0 \pm 0.00 due to higher estimated HY survival than pre-fledge survival estimates.

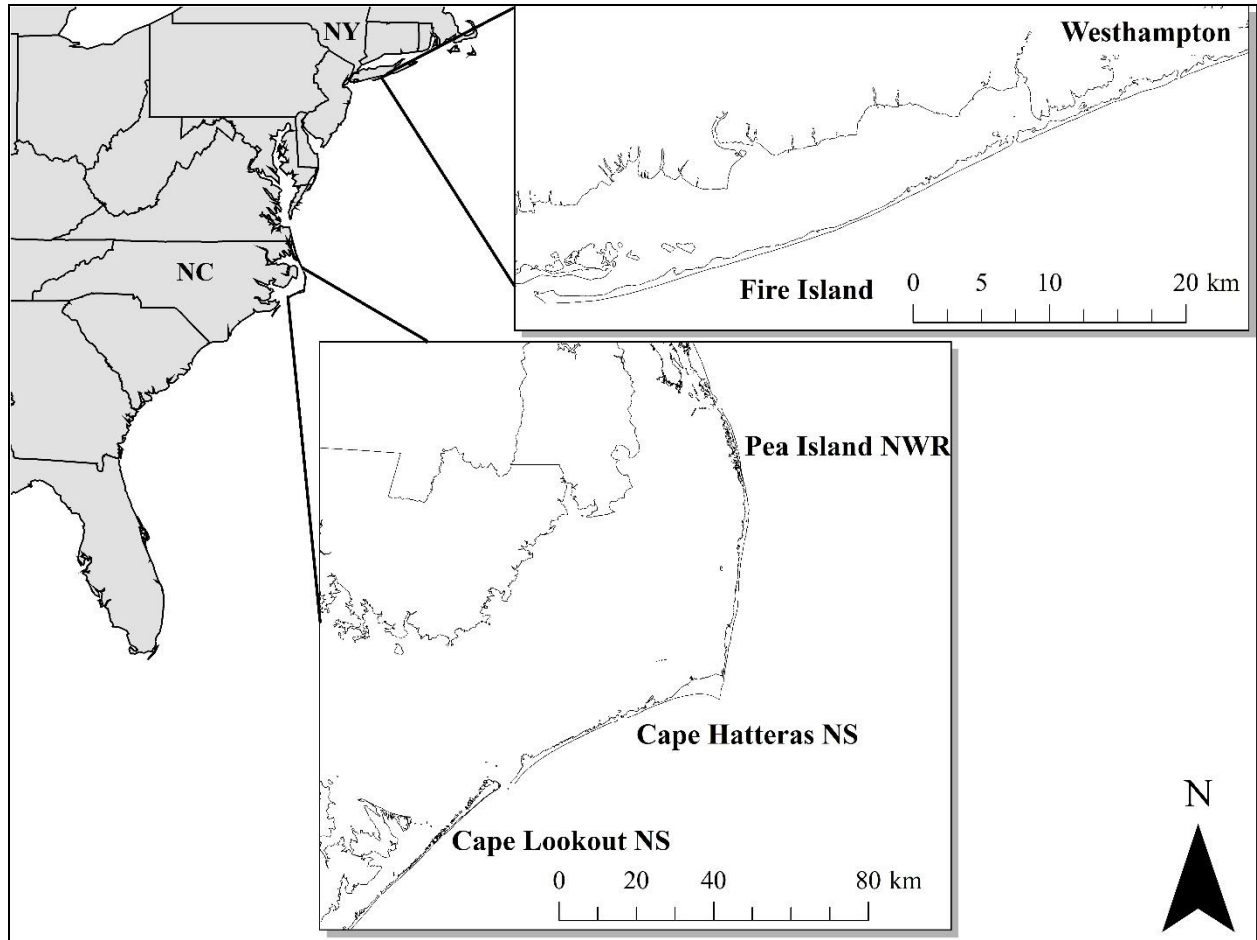


Figure 1. Map of the study area on Fire Island and Westhampton Island, New York and barrier islands of North Carolina, USA where we studied population dynamics of breeding Piping Plovers. The study took place on Fire Island 2013–2017 and in North Carolina 2015–2017.

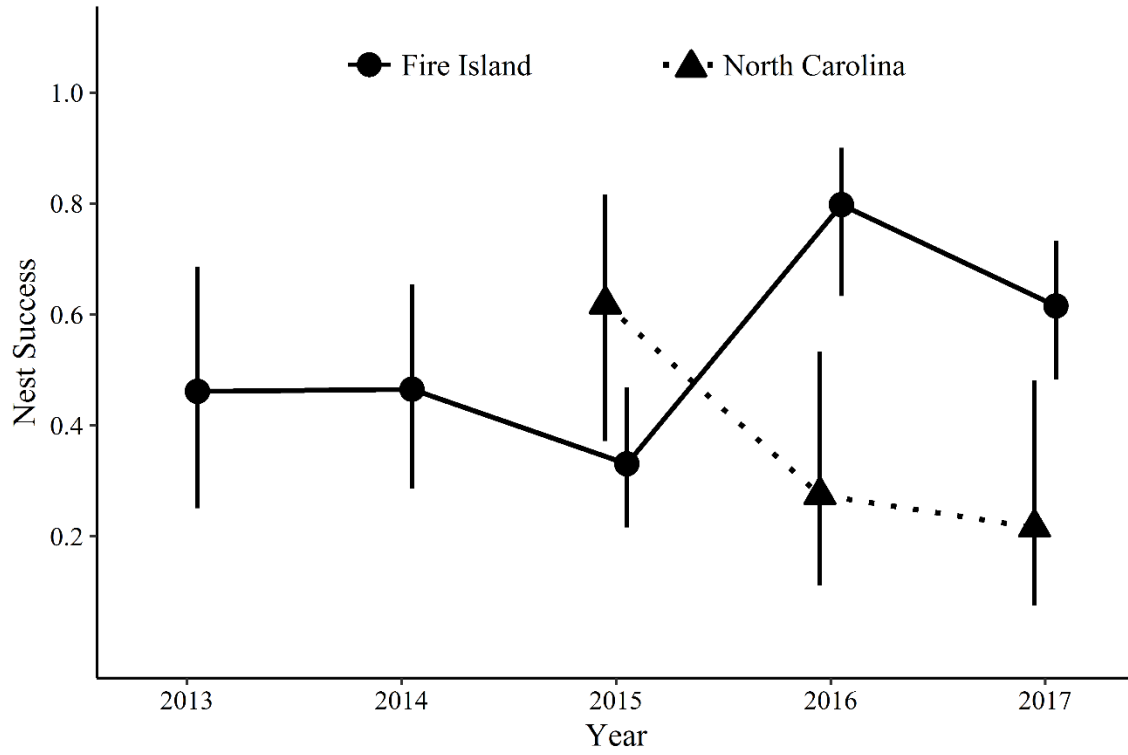


Figure 2. Estimated annual nest success of Piping Plover nests on Fire Island, NY (circles) 2013–2017 and North Carolina (triangles) 2015–2017. Error bars represent 95% confidence intervals.

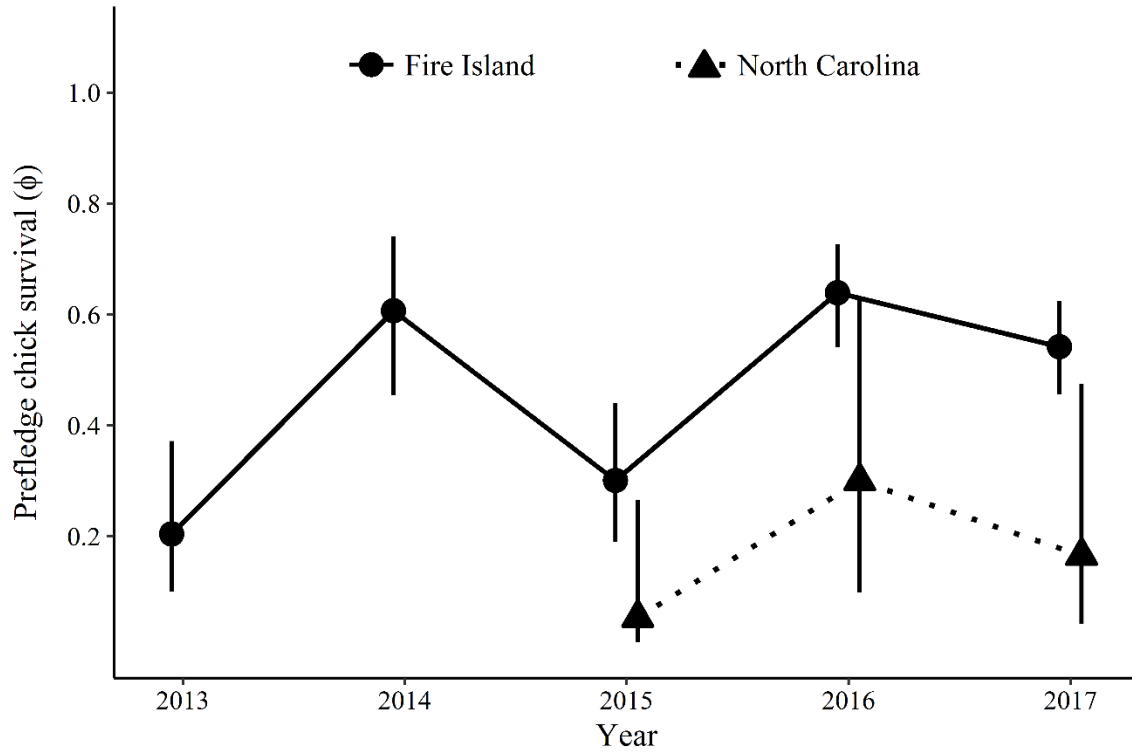


Figure 3. Pre-fledge chick apparent survival (ϕ) of Piping Plovers hatched at Fire Island, NY (circles) 2013–2017 and North Carolina (triangles) 2015–2017. Error bars represent 95% confidence intervals. Survival for Fire Island chicks was estimated using a young survival model (Lukacs 2004), and survival for North Carolina chicks was estimated using a Cormack-Jolly-Seber model (Lebreton et al. 1992).

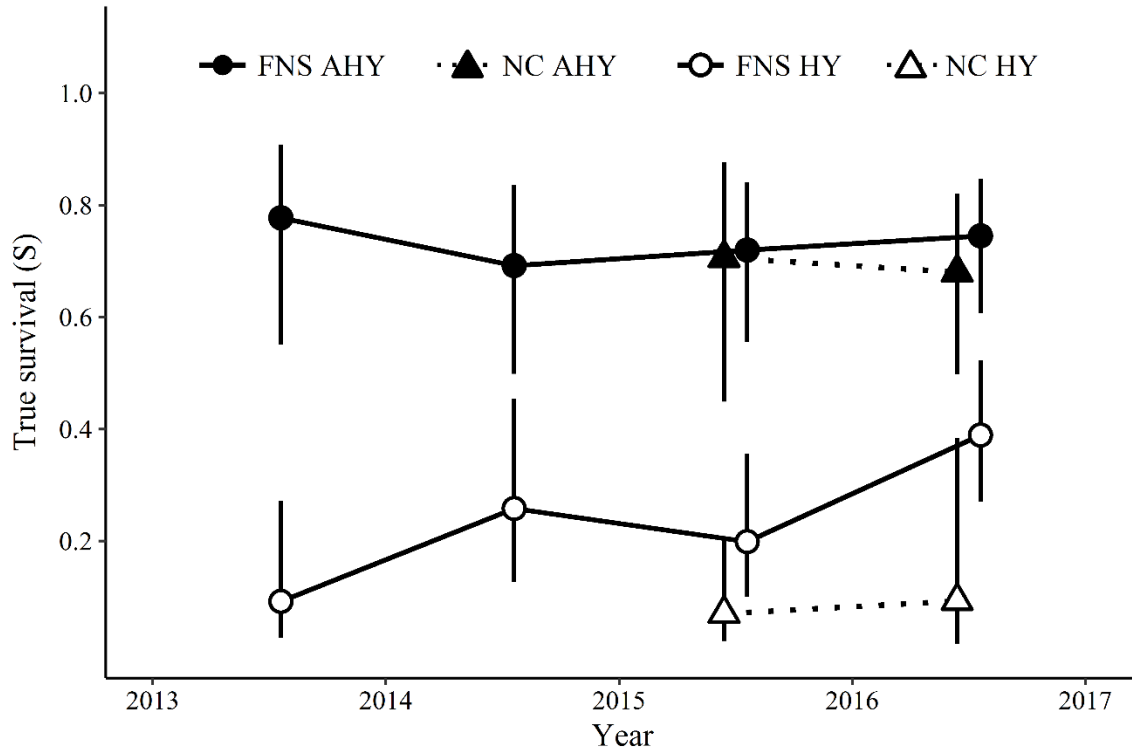


Figure 4. True survival (S) of after-hatch-year (AHY, solid symbols) and hatch-year (HY, open symbols) Piping Plovers at Fire Island, NY (FNS, circles) 2013–2017 and North Carolina (NC, triangles) 2015–2017. Error bars represent 95% confidence intervals.

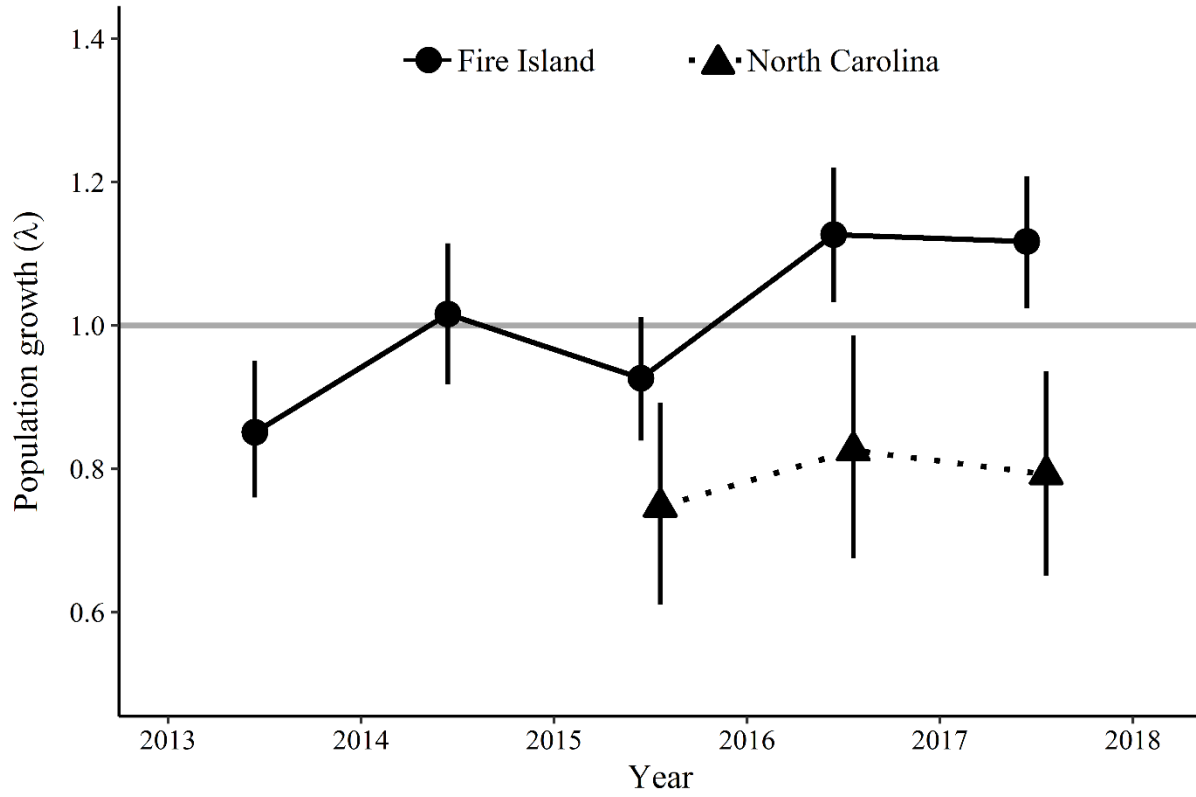


Figure 5. Population growth (λ) of breeding Piping Plovers at Fire Island, NY (circles) 2013–2017 and North Carolina (triangles) 2015–2017. The solid grey line denotes stationarity ($\lambda = 1$). Error bars represent 95% confidence intervals.

APPENDIX A

Table 2. β estimates and 95% confidence limits (CL) from a logistic exposure model (Rotella et al. 2000, Shaffer 2004) of daily survival rates (DSR) for Piping Plover nests on Fire Island, NY 2013–2017 and in North Carolina (NC) 2015–2017.

Variable	β	SE	Lower 95% CL	Upper 95% CL
Intercept ^a	4.21	0.22	3.78	4.64
Year 2013	-0.47	0.40	-1.26	0.32
Year 2014	-0.46	0.36	-1.16	0.24
Year 2015	-0.83	0.29	-1.39	-0.27
Year 2016	0.77	0.44	-0.09	1.63
NC	-1.16	0.39	-1.93	-0.40
Year 2015 \times NC	2.01	0.60	0.84	3.18
Year 2016 \times NC	-0.60	0.63	-1.84	0.65

^a Fire Island, NY 2017 DSR was the baseline in the model.

Table 3. Model ranking results of pre-fledge (0–25 day) chick survival (φ) and resight rate (p) of Piping Plover chicks from Fire Island, NY 2013–2017 and North Carolina 2015–2017. Survival for North Carolina chicks was estimated in 5-day intervals using a Cormack-Jolly-Seber model (Lebreton et al. 1992), and for Fire Island chicks with daily encounters in a young survival model (Lukacs et al. 2004). Models shown for each site are those with ≥ 0.01 model weight (w_i).

φ	p	K ^a	ΔAICc	w_i^b	Deviance
North Carolina					
Time + year ^c	Constant	5	0	0.52	7.90
Time \times year	Constant	7	0.68	0.37	3.96
Time + year	Time + year	8	3.58	0.09	4.46
Time \times year	Time + year	10	6.87	0.02	2.80
Time + year	Time \times year	10	8.53	0.01	4.46
Fire Island					
Time ² \times year ^d	Time ² \times year	30	0	0.95	2,898.87
Time \times year	Time ² \times year	25	5.77	0.05	2,915.01

^a Number of model parameters.

^b Akaike model weight.

^c Minimum AICc = 108.75. Time refers to linear time trend.

^d Minimum AICc = 3,680.18. Time² refers to quadratic time trend.

Table 4. Model ranking results from Step 1 of the Barker (1997) model for Piping Plover after-hatch-year and hatch-year (HY) true survival, resight rate (p), probability of being detected and surviving during the supplemental period (R), and probability of being detected and dying during the supplemental period (R') at Fire Island, NY 2013–2017 and in North Carolina 2015–2017. For all models, we set true survival (S) and fidelity (F) to $\text{HY} \times \text{year}$, and we fixed rate of dead recovery (r) and return rate of emigrated individuals (F') to 0.

p	R	R'	K^a	ΔQAICc^b	w_i^c	QDeviance ^d
Constant	HY + Year	HY	27	0.00	0.35	215.95
HY	HY + Year	HY	28	0.93	0.22	214.79
Constant	HY	HY	23	2.71	0.09	227.00
Constant	HY + Year	Constant	26	3.18	0.07	221.22
HY	HY	HY	24	3.58	0.06	225.79
HY	HY + Year	Constant	27	4.51	0.04	220.47
Constant	HY \times Year	HY	31	4.53	0.04	212.10
Constant	Year	HY	26	4.60	0.03	222.65
HY	HY \times Year	HY	32	5.17	0.03	210.63
HY	Year	HY	27	5.49	0.02	221.45
Constant	HY	Constant	22	6.61	0.01	232.98
Constant	Year	Constant	25	7.20	0.01	227.33
Constant	Constant	HY	22	7.26	0.01	233.62
Constant	HY \times Year	Constant	30	7.57	0.01	217.24
HY	HY	Constant	23	7.90	0.01	232.18

HY	Constant	HY	23	8.10	0.01	232.39
HY	Year	Constant	26	8.49	0.00	226.53
HY	HY × Year	Constant	31	8.86	0.00	216.43
Constant	Constant	Constant	21	10.36	0.00	238.80
HY	Constant	Constant	22	11.59	0.00	237.96

^a Number of model parameters.

^b Minimum QAICc = 1,644.42.

^c Akaike model weight.

^d Quasi-Deviance after correcting for overdispersion ($\hat{c} = 1.20$).

Table 5. Model ranking results for the Barker (1997) survival model of true survival (S), offsite resight rate (R), and fidelity (F) for after-hatch-year (AHY) and hatch-year (HY) Piping Plovers on Fire Island, NY (FNS) 2013–2017 and in North Carolina (NC) 2015–2017. Models shown are those with ≥ 0.01 model weight (w_i). For all models, resight rate (p) and probability of being detected and dying during the supplemental period (R') were held constant, and the rate of dead recoveries (r) and return rate of emigrated individuals (F') were fixed to 0.

S^a	R	F	K^b	ΔQAICc^c	w_i^d	QDeviance ^e
FNS \times HY + NC(AHY(2016 + 2017)) + FNS(HY \times year)	HY	HY	20	0.00	0.29	1,593.73
FNS \times HY + NC(AHY(2016 + 2017)) + FNS(HY \times year)	HY + NC	HY	21	0.23	0.26	1,591.89
FNS \times HY + NC(AHY(2016 + 2017)) + FNS(HY \times year)	HY	NC + HY	21	1.67	0.13	1,593.33
FNS \times HY + NC(AHY(2016 + 2017)) + FNS(HY \times year)	HY + NC	NC + HY	22	1.73	0.12	1,591.32
NC + HY \times year	HY	HY	17	3.36	0.05	1,603.27
NC + HY \times year	HY	NC + HY	18	3.63	0.05	1,601.49
NC + HY \times year	HY + NC	HY	18	4.47	0.03	1,602.32

NC + HY × year	HY + NC	NC + HY	19	4.54	0.03	1,600.33
FNS × HY + NC(AHY(2016 + 2017)) + FNS(HY × year)	HY	NC + HY + year	24	7.14	0.01	1,592.58
FNS × HY + NC(AHY(2016 + 2017)) + FNS(HY × year)	HY + NC	NC + HY + year	25	7.20	0.01	1,590.55

^a Structures with () indicate nested effects.

^b Number of model parameters.

^c Minimum QAICc value = 1,634.41.

^d Akaike model weight.

^e Quasi-Deviance after correcting for overdispersion ($\hat{c} = 1.20$)

^f Year 2013 was the baseline for year

Table 6. β estimates for the top-ranking model for true survival (S), resight rate (p), detection probability given survival during the supplemental period (R), detection probability given individual died during the supplemental period (R'), and fidelity (F) of hatch-year (HY) and after-hatch-year Piping Plovers at Fire Island, NY (FNS) 2013–2017 and North Carolina (NC) 2015–2017. Dead recovery rate (r) and the return rate of emigrated individuals (F') parameters were fixed to 0 in this model.

Parameter	Variable	β	SE	Lower 95% CL	Upper 95% CL
S	Intercept	1.01	0.55	-0.08	2.10
	FNS	0.23	0.76	-1.26	1.73
	HY	-3.68	0.86	-5.36	-2.00
	FNS \times HY	0.15	1.21	-2.22	2.51
	FNS \times 2014	-0.43	0.69	-1.79	0.93
	FNS \times 2015	-0.35	0.64	-1.60	0.90
	FNS \times 2016	-0.21	0.62	-1.42	0.99
	FNS \times 2017	-1.40	0.67	-2.71	-0.09
	CAHA \times AHY \times 2016	-0.17	0.73	-1.60	1.27
	CAHA \times AHY \times 2017	-10.59	1014.07	-1998.17	1976.99
	FNS \times HY \times 2014	1.67	1.05	-0.39	3.72
	FNS \times HY \times 2015	1.26	1.01	-0.71	3.24
	FNS \times HY \times 2016	2.06	0.94	0.21	3.91

	FNS × HY × 2017	2.99	1.01	1.02	4.96
<i>p</i>	Intercept	1.98	0.34	1.30	2.65
<i>R</i>	Intercept	0.93	0.17	0.60	1.25
	HY	1.04	0.47	0.11	1.96
<i>R'</i>	Intercept	-1.24	0.18	-1.60	-0.88
<i>F</i>	Intercept	2.41	0.44	1.54	3.28
	HY	-0.94	0.69	-2.28	0.41

**CHAPTER 2: PIPING PLOVER BROOD MOVEMENT RATES AND THEIR RELATIONSHIP TO
CURRENT MANAGEMENT PRACTICES IN PARTS OF NORTH CAROLINA**

Formatted for submission to *Journal of Field Ornithology*

Piping Plover brood movement rates and their relationship to current management practices
in parts of North Carolina

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Precocial chicks are able to walk soon after hatch. This mobility can allow chicks to move into dangerous areas, including where people drive. At Cape Hatteras National Seashore and Pea Island National Wildlife Refuge, North Carolina, USA the precocial Piping Plover (*Charadrius melodus*) is managed with vehicle and pedestrian exclusion buffers to reduce the potential for anthropogenic disturbance and mortality. From 2015–2017, we monitored broods from hatch until fledging age (25 days), and recorded brood location, chick behavior, and nearby potentially disturbing predators, people or vehicles. We estimated daily pre-fledge movements and evaluated the relationship between hourly movement rates, habitat selection, and naturally occurring potential disturbance sources. Daily brood movements were variable ($\bar{x} = 71.5\text{m}/24\text{hr}$, $\text{SD} = 70.6$, range = 0.0–327.2m), and were not significantly related to brood age ($\beta_{\text{age}} = 0.25$, 95% CI: –0.08–0.57), weather ($\beta_{\text{precipitation}} = 0.04$, 95% CI: –0.28–0.36; $\beta_{\text{max temp}} = 0.20$, 95% CI: –0.12–0.52), or annual effects ($\beta_{2017} = -0.55$, 95% CI: –1.30–0.19; $\beta_{2016} = 0.01$, 95% CI: –0.78–0.79; Year 2015 was the intercept). Hourly movement rates were also variable ($\bar{x} = 183.3\text{m}/\text{hr}$, $\text{SD} = 262.3$, range = 0.2–1450.9) and not well described by factors we tested. Predicted and observed rates of brood movement suggest regular monitoring by managers is needed to maintain the current size of buffers without exposing broods to risks from human beach users. However, the effect of these buffers on chick survival is unknown, so continued study of chick survival could benefit this small population.

Keywords: Behavior, *Charadrius melodus*, conservation, disturbance, habitat selection, management, precocial, shorebird

INTRODUCTION

Precocial birds face unique challenges before fledging. Chicks leave the nest site soon after hatching and most forage for themselves, as opposed to altricial species that remain in the nest and rely on adult provisioning for nutrition (Starck and Ricklefs 1998). The ability to move and select habitats soon after hatch allows young to access preferred foraging resources and evade predators (Starck and Ricklefs 1998, Dinkins et al. 2012) but precocial mobility also may pose risks. Movement while still unable to fly may hamper growth and survival if chicks do not acquire adequate nutrition (Scheckerman and Visser 2001). Mobile chicks also may be more noticeable to predators, or enter and move through areas that present high risks (Scheckerman and Boele 2009).

For precocial shorebirds, human recreation areas may pose high risks (Weston and Elgar 2005, DeRose-Wilson et al. 2018). Shorebird chicks can be crushed by pedestrians (Weston et al. 2012) or vehicles where beach driving occurs (Melvin et al. 1994). Chicks also can be indirectly affected by human recreation disturbance increases energy expenditure results in thermal stress (Weston and Elgar 2005) or prevents chicks from obtaining adequate nutrition (DeRose-Wilson et al. 2018). Human activities also can increase predator abundance which may negatively affect breeding (Rees et al. 2015). Given the effect that chick survival can have on population growth (Sæther and Baake 2000), managing negative effects on chicks often is a focal strategy for conserving imperiled shorebird species (Melvin et al. 1991, Weston and Elgar 2005). Management actions to reduce unnecessary energy expenditure by precocial chicks can include removing predators (Catlin et al. 2011) and human disturbance (Melvin et al. 1991), so that chicks spend less time and energy avoiding those pressures.

The Atlantic Coast Piping Plover (*Charadrius melodus*, hereafter ‘plover’) was listed as threatened under the Endangered Species Act in 1986 (U.S. Fish and Wildlife Service 1985). Many management and recovery efforts have focused on increasing reproductive output throughout the species range to achieve species recovery (Melvin et al. 1992, U.S. Fish and Wildlife Service 1996). These strategies have ranged from use of predator guards at nest sites (Melvin et al. 1992), to predator removal (Catlin et al. 2011), and to the use of exclusion zones to protect nesting and brood-rearing habitat from degradation (Schlacher et al. 2016) and human disturbance (Burger 1994).

Plover chicks are precocial, and spend 25–35 days with one or both parents before fledging (Catlin et al. 2013). During the pre-fledge period, chicks spend most of their time foraging, preferentially choosing moist sandy habitats with higher invertebrate abundance and density (Loefering and Fraser 1995, Le Fer et al. 2008a). Previous studies and observations document some plover broods traveling large distances soon after hatching to reach preferred foraging habitat (Goldin and Regosin 1998), although traveling large distances may come at a cost for chicks (Anteau et al. 2014). However, there is evidence that optimal foraging resources alone may not drive brood movement for other precocial shorebirds (Kosztolányi et al 2007, Wilson and Colwell 2010). Instead, brood movements may be driven by a combination of seeking foraging opportunities, avoiding predation and disturbance, and pressure from territorial neighbors.

Avoiding predation is a key factor in animal movements, especially while rearing young (Berger 1991, Laing and Raveling 1993, Dinkins et al. 2012). Young typically are more susceptible to predation than adults, so habitat selection may trade off optimal foraging habitats for habitats that protect or conceal young from predators (Signorell et al.

2010), or for those that may have lower predation pressure (Laing and Raveling 1993). Ideal foraging habitats for plovers typically are open, saturated sandy and muddy habitats, often only sparsely vegetated, so plover chicks must either rely on cryptic coloring to avoid detection by predators (Fraser and Catlin 2019, *in press*), or move to other habitats that provide more vegetative cover (Wiltermuth et al. 2015). Additionally, plovers often respond to human activity as they would to predators (Flemming et al. 1988, Burger 1994), potentially increasing their amount of space use when disturbed by people (Haffner et al. 2009, Wilson and Colwell 2010).

In addition to intraspecific pressures, pressures from conspecifics may result in similar movement decisions. Plovers establish and maintain territories for nesting, which also protect habitat needed during brood rearing (Wiltermuth et al. 2015, Walker et al. *in review*). In Kentish Plovers (*C. alexandrinus*), some broods selected lower quality habitats, possibly reducing the chicks' fitness, in favor of avoiding intraspecific competitors (Kosztolányi et al. 2006, 2007). However, the cost of staying in areas with high territorial conflict may be severe. Territorial adults may injure or kill young in their disputes (Kosztolányi et al. 2007, Catlin et al. 2014). If such risks are possible, plover broods may move away from nonparental adults. Plover territoriality may be related to small brood movements, as brood territory size is restricted due to dense competition around food resources (Hixon 1980). Conversely, territoriality may be related to increased movement, as subordinate adults and broods are forced to leave an area to avoid conflict (Hixon 1980, Kosztolányi et al. 2006).

Brood movements may make it difficult for managers to effectively protect habitat for plover broods, especially in areas that are popular for recreation. The use of exclusion

buffers is common to reduce the negative impact of human disturbance to shorebirds (Blumstein et al. 2003, Wilson and Colwell 2010, Schlacher et al. 2013), although their effective size may change in relation to bird fitness (Beale and Monaghan 2004), habitat selection (Yasué 2006), or other factors (see Glover et al. 2011 for review). Additionally, exclusion of people or certain activities from popular areas often is controversial, therefore, managers attempt to establish buffer sizes large enough to benefit birds while small enough so that they don't unnecessarily restrict stakeholders (Glover et al. 2011).

At Cape Hatteras National Seashore, North Carolina, USA (hereafter, 'CAHA'), management strategies have evolved for breeding plovers over the past decade. The National Audubon Society and Defenders of Wildlife filed a lawsuit against the National Park Service in 2007, which alleged inadequate resource protection of plovers and other species of concern from off-road vehicle (ORV) traffic at CAHA. A consent decree was reached among the plaintiffs, defendants, and intervenors in 2008, and it created an interim ORV management plan until a permanent management plan could be drafted (Defenders of Wildlife et al. v. National Park Service et al., [Case No. 2:07-CV-45-BO, U.S. District Court, Eastern District of North Carolina, Northern Division]). In 2012, the ORV Management Plan (ORVMP) was finalized and implemented. The ORVMP outlined management strategies for plovers that focused on three periods of the breeding season: 1) the pre-nesting period, 2) the nesting and incubation period, and 3) the brood rearing period. Within the brood rearing period, CAHA personnel manage beach closures to create dynamic exclusion buffers around plover broods. These exclusion buffers (hereafter, 'buffers') are meant to decrease or eliminate the negative impacts of anthropogenic disturbance and death caused by human recreation (Flemming et al. 1988, Burger 1994,

DeRose-Wilson et al. 2018) and beach driving (Melvin et al. 1994) at CAHA. However, maintenance of beach closures to create and maintain these buffers requires substantial personnel effort and resources (Hecht and Melvin 2009), especially if broods move often and quickly. Therefore, understanding patterns of brood movements may aid managers in efficiently providing buffers for plover broods.

In this study, we investigated the relationship among plover brood movements, behavior, and potential disturbances. Our first objective was to understand how far broods may move each day until they reach fledging age. Intensive monitoring of broods (i.e., continuous observation during daylight hours) relies on substantial staffing resources. In cases of limited staffing, brood checks may only be conducted once or twice a day, and broods may exit protected areas while not being monitored, exposing them to risks or disturbance. Ensuring that broods remain within protective buffers could help increase fledging success, even when the broods are not being actively monitored.

Second, we were interested in how quickly broods may move during observation. Management personnel observe broods to determine status and location, and they use these observations to evaluate if beach closures need to be adjusted to meet minimum buffer sizes. Continuous observation of broods can allow managers to respond to or predict rapid brood movements, especially if that movement is related to habitat choices, observed brood behavior, or potential disruptions to the brood. Therefore, we examined the relationship between these pressures and subsequent brood movement during continuous observation. This approach was used to understand if certain pressures elicit more rapid brood movements and to evaluate the potential intensity of plover brood observation necessary by managers (i.e., continuous or periodic monitoring).

METHODS

Study Area and Management

Cape Hatteras National Seashore ('CAHA'; 35.2240°N, 75.5325°W; Fig. 1) consists of approximately 70km of barrier islands on the North Carolina coast that also encompasses Pea Island National Wildlife Refuge ('PEA'; 35.7166°N, 75.4935°W; Fig. 1). By 15 March every year, CAHA personnel erect pre-nesting closures based on historic breeding activity and an evaluation of the habitat for plovers, Wilson's Plovers (*C. wilsonia*), American Oystercatchers (*Haematopus palliatus*), Least Terns (*Sternula antillarum*), Black Skimmers (*Rynchops niger*), and other colonial nesting waterbirds. The pre-nesting closures use symbolic fencing (signs and string) to exclude compliant pedestrians and vehicles to protect habitat and eliminate potential anthropogenic disturbance. These closures remain in effect until two weeks after the last sign of breeding activity of any of the target species or 15 August, whichever occurs later. When nests are located or breeding activity observed, CAHA personnel measure the distance from the nest or activity to the boundaries of the pre-nesting areas, and they expand the current boundaries to meet minimum buffer sizes, if the current distance is not sufficient. In cases where nests or breeding activities are detected outside of pre-nesting areas, new fencing is erected to meet minimum buffer sizes, and this new fencing may be incorporated into other existing closures, if these areas overlap.

Plover broods are protected from anthropogenic disturbance from hatch until fledging using buffers delineated with the same symbolic fencing used for prenesting closures. These buffers are dynamic such that CAHA personnel move the closed areas as the broods travel. In 2015, in accordance with the ORVMP, plover broods were protected from ORV traffic with 1000m buffers and from pedestrian traffic with 300m buffers. The Defense

Authorization Act of Fiscal Year 2015 (30 USC §3057) required the National Park Service to review and reduce resource buffers as much as possible without negatively affecting the resource. Subsequently, the buffers around plover broods were reduced to 200–500m for ORVs and 100m for pedestrians beginning in 2016. ORV buffers are set at 200m if resource staff are able to provide continuous observation of broods, and they are extended to 500m if that monitoring effort is absent. In many cases, buffer sizes for plover broods may have already been met by prenesting closures or closures for other target species, so broods may have been present in closed areas that were larger than the prescribed buffer sizes (Fig. 2).

Similar protective measures are used at PEA, although buffer sizes are determined at the discretion of Refuge biologists. While brood checks occur nearly daily, there rarely is continuous daylight brood observation (B. Van Druten, USFWS, personal communication). There is no vehicular beach traffic at PEA, although North Carolina state highway 12 (NC-12) runs through the entirety of the Refuge behind the primary dune line. Our study area comprised ocean-front sandy beaches, dunes, ephemeral pools, retention ponds, and beaches and tidal flats on Pamlico Sound which bounds the western edge of CAHA and PEA.

Field Methods

We searched for nests daily from April through July, 2015–2017 by monitoring breeding behavior and locating incubating birds. After nest discovery, we recorded location coordinates using a Trimble GEO XT unit (Trimble Systems Ltd., Sunnyvale, CA) with the WGS 1984 datum. We attempted to check all known nests every 1–3 days until hatch or nest failure.

We banded plover chicks as soon after hatch as possible, usually before they left the nest cup. Chicks were banded with field-readable coded green Darvic flags on one upper leg and an etched orange Darvic band on the opposite upper leg. We measured mass (nearest 0.1g), tarsus length and culmen length (nearest 0.1mm), and wing chord (nearest 1mm). We did not directly approach broods again until they reached 22–25 days old, when we recaptured chicks by hand using butterfly nets and again measured and weighed them and assessed their condition, including leg health, prior to fledging.

We attempted to locate broods and resight banded chicks every 1–3 days for 30 days post-hatch, regardless of when the brood was last observed. We searched through brood-rearing habitat near the nest site and where the brood was last observed. When we found a brood, we calculated its location coordinates from a distance. We offset the coordinates at our location, determined by GPS, using distance to the brood estimated with a laser rangefinder (Nikon Aculon AL11, $\pm 1\text{m}$ advertised accuracy, Nikon Americas, Melville, NY) and bearing to the brood using a handheld compass. This method allowed us to collect locations without approaching a brood and affecting the bird's behaviors (S.G. Robinson, Virginia Tech, unpublished data). If members of a brood were $>100\text{m}$ apart, we located each of the groups. We observed a randomly selected chick for 5 min, during which we recorded the number of foraging attempts (pecks), and we recorded behavior (forage, stand, walk, sit, chase, flee, brood, crouch, preen, other) every 10 seconds. We recorded the habitat (wet sand, dry sand, wet vegetation, dry vegetation, and wrack) in which the chicks were located. We based our habitat classification on dominant habitat type within $\sim 2\text{m}$ radius from the chick. We observed chicks from a distance not likely to disturb them ($>80\text{m}$, DeRose-Wilson et al. 2018). If a chick moved out of sight, we continued the sample and

noted at each 10 second interval that the chick was not visible. If the chick was out of sight for 60 consecutive seconds, we terminated the sample.

Immediately after completing a chick behavior sample, we recorded counts of potential disturbance sources (e.g., non-parental plovers, Killdeer [*C. vociferous*], pedestrians, vehicles, gulls [*Larus spp*], crows [*Corvus spp*], ghost crabs [*Ocyrode quadrata*], dogs [*Canis lupis familiaris*], or other possible predators) within 500m of our location. We estimated distances to each using the rangefinder, and we recorded the count of each in 100m intervals. In 2015, if a brood moved >100m during our observation period, we again recorded brood location, behavior, and potential disturbance. In 2016–2017, we attempted to collect at least two locations, behavior samples, and disturbance samples per observation day, regardless of distance the brood moved during the observation.

Analytical Methods

Daily Movement

To calculate movement on the scale of days, we used daily brood locations from 2015–2017. If a brood was located more than once per day, we used the last location observed for that day. We calculated the Euclidean distance between consecutive brood locations on different days using the package ‘*geosphere*’ (Hijmans 2017) in statistical program R (R Core Team 2018), and we scaled the distance using the intervening time between observations. For the first location, we used the nest coordinates and calculated the distance to the first observation of chicks, as some chicks were first observed outside of the nest cup. Since the time between our observations was variable, we used the average age of the brood between the two observations. We used locations for broods aged 0–25 days (the

average time to fledging, U.S. Fish and Wildlife Service 1996, Catlin et al. 2013, DeRose-Wilson et al. 2018, Hunt et al. 2018). We predicted that daily movements would increase with age as chicks become more mobile and more likely to flee to evade predators (Ruthraff and McCaffery 2005, Colwell et al. 2007), but that movements might also follow a quadratic curve with age, as chicks reach and then remain at foraging territories (Wilson and Colwell 2010).

To test for the potential effect of environmental variables on brood movement, we included daily maximum temperatures and daily precipitation, obtained from the Billy Mitchell Airfield weather station (35.23° N, 75.61° W, <https://www.ncdc.noaa.gov>, Fig. 1). We predicted that brood movement would decrease with increasing temperatures, as broods may avoid expending energy during high temperatures (Kuklinkski et al. 1996). We predicted that brood movement would be negatively related to precipitation, which may provide ephemeral pools for foraging and increase prey activity and availability (Berridge 2012), reducing the distance chicks would need to travel for foraging resources. To control for potential seasonal changes in brood movements, we included Julian date in our models. We standardized all dependent variables to facilitate comparisons of variable effect size on movement rates. We built an *a priori* candidate set of seven models: an additive global model, four models to test for single-hypothesis effect on movement (year, age, date, weather), and we built two multivariable additive interaction models: one of quadratic age effect, and one with an additive effect of age and year. We log-transformed the response variable of meters per 24 hours to use in our regressions, and we back-transformed estimates derived from selected models. We ranked models according to ascending $\Delta AICc$ (Burnham and Anderson 2002), and we selected the top-ranked model to estimate parameters.

Hourly Movement

To investigate the rate of movements in response to environmental variables and potential disturbances, we used brood location and behavioral data, and environmental observations in the area surrounding broods that were recorded during a single continuous observation period (≥ 2 locations per observation period). We calculated the Euclidean distance between consecutive brood locations during a single observation, and we scaled the distance using the intervening time between the consecutive observations (m/hr).

We used behavioral and environmental data collected at the first brood location during the observation period as independent variables that could influence the rate of brood movement to the second location (Table 1). Since broods sometimes used different habitats during a behavior sample, we used the most frequently-used habitat type during each sample to represent habitat type for that observation (Table 1). Since we did not observe broods in densely vegetated habitats ($>75\%$ ground cover), and we assumed there was unlikely any response-related difference (e.g., perceived predation risk) between sparsely- and moderately vegetated habitats of the same type, we simplified habitat type during observation into wet or dry habitats. We calculated foraging rate (pecks per minute, 'ppm') for each sample period. We combined the observed instantaneous behaviors into four categories: disturbed, undisturbed, foraging, and other (Table 1). We calculated the proportion of time spent exhibiting these behaviors after removing the time spent out of sight (i.e., proportion of time of unknown behaviors) in each observation.

We calculated the density (individuals per 100m^2) of five known disturbers (ghost crabs, avian predators, humans and vehicles, adult Killdeer, and adult plovers that were not

the parents of the observed brood, Goldin and Regosin 1998, CEW personal observation). We observed few dogs or other mammalian predators during our counts, so we did not include them in our analysis. We standardized all independent variables.

We log transformed brood movement per hour and built a null model which included a linear relationship with age, based on modeling daily movements. We built a candidate set of models to test several hypotheses. We hypothesized three observable factors could relate to the rate of brood movements: brood habitat selection, behavior, and potential disturbance presence (Table 1). We built three models to each test an hypothesis, and a fourth model testing the additive interaction of age and foraging rate (pecks per minute), as foraging rate may represent behavior and habitat interactions (Loefering and Fraser 1995, Goldin and Regosin 1998). We then built additive interaction models of predator-habitat and behavior-habitat combinations. We hypothesized that foraging rate may interact with time spent exhibiting other behaviors, and foraging rate may also mitigate the effect to which broods responded to potential disturbance sources. We also hypothesized those same behavior and potential disturbance sources may differently affect brood movement depending on the brood's selected habitat. We did not include correlated variables (Pearson's $|r| > 0.60$) in the same model, except in the global model, which included additive interactions of all independent variables. We ranked our *a priori* candidate set of 10 models according to ascending $\Delta AICc$. We used model rankings to compare relative importance of each of our competing hypotheses. We evaluated direction and overall significance of coefficient estimates and confidence intervals as evidence to support our hypotheses, even if models were uncompetitive or less informative (Arnold 2010). We used parameter estimates from the top model to make predictions about brood movement rates.

RESULTS

From 2015–2017, we monitored 19 broods and logged 20.75 observation hours. We collected 191 brood locations (Fig. 2), 132 behavioral samples, and 113 disturbance environment samples. Most chicks were observed within the boundaries of pre-nesting closures (Fig. 2), and all chicks were observed within some type of protective closure or buffer. During the study period, six broods (31.5%) fledged at least one chick. We observed two chick mortalities, both caused by ghost crab depredation.

Daily Brood Movement

We estimated 96 daily movements from 19 broods in 2015–2017. Our mean visit interval was 2.1 days (SD = 1.0, median = 2.0, range = 0.22–4.8). Mean daily maximum temperature was 28.9°C (SD = 2.12, range = 20–33.9), and average daily rainfall was 1.92cm (SD = 14.58, range = 0–24.6). Mean brood age at the time of observation was 7.8 days (SD = 7.8), and mean daily movement was 71.5m/24hr (SD = 70.6, range = 0.0–327.2m). Most (69.8%) daily movements were <100m, and all daily movements were <500m (Fig. 3).

The null model of age was the most parsimonious descriptor of daily brood movement, but age was not a significant predictor of movement (Fig. 4; $\beta_{\text{age}} = 0.25$, 95% CI: -0.08–0.57), and there was substantial additional variation left unexplained (adjusted $R^2 = 0.01$). There was little evidence to support our hypotheses of weather, annual, or seasonal effects on brood movement (Table 3). Daily movement was somewhat smaller in 2017 ($\beta_{2017} = -0.55$, 95% CI: -1.30–0.19) than in other years ($\beta_{2016} = 0.01$, 95% CI: -0.78–0.79, Year 2015 was the intercept). Date was invariant with daily movement rates ($\beta_{\text{date}} = 0.03$, 95% CI: -0.29–0.35). Support for daily weather conditions was mixed: precipitation was unrelated to

movement ($\beta_{\text{precipitation}} = 0.04$, 95% CI: -0.28–0.36), but temperature had a weak but insignificant positive relationship ($\beta_{\text{max temp}} = 0.20$, 95% CI: -0.12–0.52).

Hourly Movement

Broods, on average, spent most of their time undisturbed, followed by less time foraging (Table 3). Time spent being disturbed was the least observed behavior (Table 3). We observed eight encounters with potential disturbance sources that elicited disturbance behavior from the focal chick. Of these encounters, three (37.5%) were with birds, two (25%) with other adult plovers, two (25%) with heterospecific shorebirds (Killdeer and Black-bellied Plover [*Pluvialis squatarola*]), and one (12.5%) with a ghost crab. We saw no disturbed behavior that could be tied to encounters with humans or vehicles. All people observed during these observations were outside the exclusion buffer sizes in use at CAHA, except for approved resource management personnel and vehicles, and where NC-12 occurred at PEA, where one brood was present in 2017. Mean densities of potential disturbance sources were similar across source types, but the range of observed densities was large for some sources (Table 4). Anthropogenic sources were the most commonly observed potential disturbance source, although this varied by location and year (Supplemental Table S1).

We estimated 68 movement distances from 7 broods in 2016–2017. Mean hourly movement was 183.3m/hr (SD = 262.3, range = 0.2–1450.9). Nearly half (48.5%) of observed movements were <100m per hour, and most (91.1%) observed movements were <500m per hour (Fig. 4).

Brood hourly movement was best described by our null model of brood age (Table 5), but there was little evidence that movement rates increased as broods aged ($\beta_{\text{age}} = 0.03$, 95% CI: -0.29–0.34; adjusted $R^2 = -0.01$).

Overall, there was little support for other hypotheses regarding hourly brood movement rates (Table 5). Broods moved more slowly when they occupied wet habitat ($\beta_{\text{wet}} = -0.19$, 95% CI: -0.52–0.15) versus dry habitat. Broods moved slower after more disturbed behavior ($\beta_{\text{disturbed}} = -0.20$, 95% CI: -0.54–0.13) and faster after spending more time undisturbed ($\beta_{\text{undisturbed}} = 0.33$, 95% CI: -0.02–0.67) or exhibiting other behaviors ($\beta_{\text{other}} = 0.02$, 95% CI: -0.31–0.36). Broods also moved slower after they foraged at higher rates ($\beta_{\text{ppm}} = -0.11$, 95% CI: -0.49–0.27). According to model rankings, observed potential disturbance sources appeared to be the least supported of our hypotheses regarding movement rates, both alone and when interacting with habitat (Table 5).

DISCUSSION

Our results suggest that plover brood movement is variable, both on a daily and hourly scale, and potential environmental factors were not significant predictors of brood movement rates. Most observed daily and hourly movement distances were as large as or smaller than current management buffer sizes.

Our modeling suggested that brood age was the most parsimonious descriptor of daily and hourly brood movements, though there was substantial variation left unexplained by these models. While we did not detect a significant relationship between age and movement in this study, age has been previously thought to influence movement distances of shorebird chicks. Brood movement of other *Charadriidae* species has been negatively

related to brood age, perhaps driven by large movements post-hatch to reach optimal habitats (Knopf and Rupert 1996, Wilson and Colwell 2010). However, Western Sandpiper (*Calidris mauri*) chicks moved larger distances as they aged, possibly due to a greater ability to thermoregulate and evade predators (Ruthrauff and McCaffery 2005). We thought that plover broods would be driven by a combination of these pressures, hence our additional hypothesis of a quadratic age effect, but brood movement was neither well described by this pattern, nor by a simple linear relationship with age.

There was little evidence that weather conditions affected brood movements in this study. Ambient temperature can restrict activity in precocial chicks, although this relationship typically has been examined with low ambient temperatures (Krijgsveld et al. 2003a, b, Schekkerman and Boele 2009). However, plover brood activity was hypothesized to possibly be restricted in North Carolina due to extreme heat, although there had not been evidence to support this hypothesis in the past (Kuklinkski et al. 1996). Ambient temperatures in North Carolina during the breeding season are more similar to chick body temperatures (~38–40°C, Bakken et al. 2002) than those experienced by arctic breeding species (July average temperature: 15–19°C in Churchill, Manitoba, Canada, Krijgsveld et al. 2003a) or experimentally controlled temperatures (~7°C and 25°C, Krijgsveld et al. 2003b). Therefore, heat loss in North Carolina plover chicks likely occurs more slowly than in Arctic breeding species (Krijgsveld et al. 2003a). Precipitation also may increase heat loss, but this effect is usually in concert with low temperatures (Krijgsveld et al. 2003a). The weak relationship between movement and temperature suggests thermal stress is unlikely to be a risk to North Carolina plover chicks. Accordingly, plover chicks in North Carolina may

rarely face energetically-costly climatic conditions, and thus would not have to alter their energy expenditure to avoid temperature stress.

Neither the hypothesis of annually-driven habitat changes, nor the day-specific effects of precipitation were supported as predictors of brood movement. At our study site in 2016, rainfall from Tropical Storms Bonnie and Colin caused significant flooding (~ 45cm during 29 May–7 June), creating large ephemeral pools and pond drainages that persisted for several weeks in some areas that broods used. This flooding may have made arthropod prey resources more active or available (Berridge 2012) for plover chicks. However, in 2015 and 2017, these large foraging areas were not present during the brood rearing period, although these areas commonly flood during the winter (W.P. Thompson, NPS, personal communication). We predicted that movement rates would be higher in 2015 and 2017, because broods would need to move farther to reach the limited foraging habitats (Goldin and Regosin 1998, Elias et al. 2000) in these relatively dry years. However, average daily movement rates were similar in 2015 and 2016, and movement rates were lowest in 2017. It is possible that there was enough foraging habitat in 2016 so that broods were able to shift their home range or move large distances without losing access to optimal foraging resources. For example, supplemental feeding in Texas was not related to smaller home ranges for Northern Bobwhite (*Colinus virginianus*), but instead suggested that quail shifted their home ranges to maintain access to the supplemental food source (Buckley et al. 2015). However, we are unsure why movement rates decreased in 2017 if foraging habitat availability is related to brood movement. Continued investigation into brood responses to fluctuations in habitat availability and abundance is merited.

There also was little evidence that observable potential disturbance sources affected brood movement rates. Avoidance of potential predation or disturbance was the least supported of our hypotheses, and we observed few events of a known potential disturbance source's effect on a chick's behavior. However, there is evidence that avoidance does affect movement in some way for shorebirds. Human recreation is related to increased space use in breeding Piping Plovers (Haffner et al. 2009) and movement distance in Snowy Plover (*C. nivosus*) broods (Wilson and Colwell 2010); however, these studies examined human recreation as categorical effects, and not as discrete events, as in this study. It is possible that plover brood movement may still be affected by potential disturbance sources, but the effect may manifest in larger cumulative pre-fledge movements (i.e., larger home range), instead of broods altering their rates of movement after a disturbance event. Additionally, the effects of disturbed and undisturbed behaviors on movement rates were the opposite of what we predicted. Instead of leaving an area of danger or conflict, plover chicks at CAHA may alter other activities while in the presence of humans or potential predators (Burger 1994, Loegering and Fraser 1995, Goldin and Regosin 1998).

Rates of disturbed behavior were much lower than undisturbed behaviors. Known sources of disturbance that we observed were typically very close to the brood (<20m, CEW, personal observation), but we were unable to assign many instances of disturbed behavior to a specific cause. We did not observe any instances of disturbance known to have been caused by humans, nor did we observe any people within the managed buffers, although we often did observe footprints within closed areas. Thus, anthropogenic sources did not appear to be an important disturbance factor during this study under the current management strategies. However, often plover broods were protected by closed areas that

were larger than the minimum buffer sizes, due to the size of pre-nesting closures or buffers used for breeding activity of other species nearby (Fig 2). Because closed areas sometimes were altered for other species, we were unable to directly examine the relationship between brood movement, behavior, and the different buffer sizes.

A common method for evaluating disturbance thresholds involves measuring the distance at which certain stimuli (i.e., human presence or activities) disturb birds, called flush or flight initiation distance (FID; Blumstein et al. 2003, Beale and Monaghan 2004). These distance thresholds are then used to create exclusion buffer sizes (Blumstein et al. 2003, Burger et al. 2009). While there has been a considerable body of work examining distance of human disturbance to incubating birds (e.g., Flemming et al. 1988, Burger et al. 2009, St Clair et al. 2010, Borneman et al. 2016), there is little data examining chick behavior using these methods, where distances from known disturbance sources are explicit. According to Flemming et al. (1988), plover chicks appeared to alter their behavior when humans approached to within 160m of their location, but not so to vehicles, even when vehicles were <2m away. Colwell et al. (2007) approached Snowy Plover broods to assess their response to pedestrian disturbance, but they did not report the distances that elicited chick reactions. Concerns regarding disturbance and its effects on plover broods (Flemming et al. 1988, Burger 1994, Loegering and Fraser 1995, DeRose-Wilson et al. 2018), especially given their imperiled status, may preclude experimental efforts to evaluate disturbance in favor of observational methods, similar to this study. Nonetheless, continued efforts to evaluate disturbance threshold distances for broods could benefit plover chicks.

Many observed hourly brood movement were larger than predicted daily movements. Similar to the function of home range centers in other species (Chamberlain et

al. 2003), broods may make multidirectional movements at variable rates of speed while remaining in relatively small areas. Unlike other bird species whose activities center on the nest site (Vitz and Rodewald 2010), plover broods rarely return to the nest site, and instead their day-to-day center of activity may be more flexible. The speed with which broods can move during short periods creates the potential for broods to quickly reach the boundaries of buffers that are currently being used at CAHA. This can quickly expose them to dangerous ORV traffic (Melvin et al. 1994) or other anthropogenic-related risks such as dogs or trampling by pedestrians without intervention by management personnel if left unmonitored. Although we did not observe any brood outside of a protective buffer during the study, even with the largest buffer sizes used through 2015 (1000m), given the observed movement rates, broods could walk out of the buffer in less than 24 hours. This result underscores the importance of regular monitoring if buffer sizes remain as they were during this study.

For plovers in North Carolina, reproductive output has rarely attained the rate needed for a stationary population (1.07 fledged chicks per pair, Weithman et al. *in review*) or the reproductive rate of 1.5 fledged chicks per pair listed as a species recovery goal (U.S. Fish and Wildlife Service 1996, Schweitzer 2017). The reproductive rate at CAHA also remained below these rates and did not appear to respond to implementation of the exclusion buffers (NPS, unpublished data, Schweitzer 2017), although there is some evidence the breeding population increased after implementation of the ORVMP (E. Kwon, Virginia Tech, unpublished data). This result suggests that other factors such as habitat availability (Robinson et al. *in review*) or predation (Loefering et al. 1995, Kwon et al. 2018) also may be affecting plover chick survival. While brood-occupied habitat did not have

significant relationship with movement rates in this study, increasing the amount of and the access to preferable moist sand foraging habitats may reduce the distance broods must move to reach those habitats (Goldin and Regosin 1998). Nearer foraging resources that are more easily accessed could improve growth rates (Anteau et al. 2014) and, by extension, chick survival (Catlin et al. 2013). Given the well-understood benefit of moist sand habitats to plover chick survival (Loegering and Fraser 1995, Goldin and Regosin 1998, Le Fer et al. 2008b, Catlin et al. 2013, DeRose-Wilson et al. 2018), and its continued positive effects on survival after chicks have fledged (Catlin et al. 2014), management to increase and improve foraging habitats for plover chicks may have lasting effects on the population.

ACKNOWLEDGEMENTS

Funding for this study was provided by The National Park Service. We thank Cape Hatteras National Seashore and Pea Island National Wildlife Refuge for permission to work on their properties. We thank D. Hallac, R. Harrison, B. Muiznieks, and S. Siegler for support of this work. We are grateful to the many permanent and seasonal staff at both locations for their communication and logistical support, as well as members of the Virginia Tech Shorebird Program for support during all stages of this study. We thank A. Etherington and K. Walker for their hard work and enthusiasm during data collection. This work was conducted under U.S. Geological Survey Bird Banding Permit #21446, U.S. Fish and Wildlife Service Endangered Species Permit #TE-103272-3, North Carolina Wildlife Resource Commission Endangered Species Permit #00438, and Virginia Tech IACUC protocol #16-244.

LITERATURE CITED

- ANTEAU, M.J., M.T. WILTERMUTH, M.H. SHERFY, T.L. SHAFFER and A.T. PEARSE. 2014. The role of landscape features and density dependence in growth and fledging rates of Piping Plovers in North Dakota, USA. *The Condor* 116: 195–204.
- ARNOLD, T.W. 2010. Uninformative Parameters and Model Selection Using Akaike's Information Criterion. *Journal of Wildlife Management* 74: 1175–1178.
- BAKKEN, G.S., J.B. WILLIAMS and R.E. RICKLEFS. 2002. Metabolic response to wind of downy chicks of Arctic-breeding shorebirds (*Scolopacidae*). *The Journal of Experimental Biology* 205: 3435–43.
- BEALE, C.M. and P. MONAGHAN. 2004. Behavioural responses to human disturbance: a matter of choice? *Animal Behaviour* 68: 1065–1069.
- BERGER, J. 1991. Pregnancy incentives, predation constraints and habitat shifts: experimental and field evidence for wild bighorn sheep. *Animal Behaviour* 41: 61–77.
- BERRIDGE, M.J. 2012. Osmoregulation in terrestrial arthropods. In: *Chemical Zoology* (M. Flotkin & B.T. Scheer, eds.), pp. 287–320. Academic Press, Cambridge, MA.
- BLUMSTEIN, D.T., L.L. ANTHONY, R. HARCOURT and G. ROSS. 2003. Testing a key assumption of wildlife buffer zones: is flight initiation distance a species-specific trait? *Biological Conservation* 110: 97–100.
- BORNEMAN, T.E., E.T. ROSE and T.R. SIMONS. 2016. Off-road vehicles affect nesting behaviour and reproductive success of American Oystercatchers *Haematopus palliatus*. *Ibis* 158: 261–278.

- BUCKLEY, B.R., A.K. ANDES, B.A. GRISHAM and C. BRAD DABBERT. 2015. Effects of broadcasting supplemental feed into roadside vegetation on home range and survival of female northern bobwhite. *Wildlife Society Bulletin* 39: 301–309.
- BURGER, J. 1994. The Effect of Human Disturbance on Foraging Behavior and Habitat Use in Piping Plover (*Charadrius melodus*). *Estuaries* 17: 695–701.
- BURGER, J., M. GOCHFELD, C.D. JENKINS and F. LESSER. 2009. Effect of Approaching Boats on Nesting Black Skimmers: Using Response Distances to Establish Protective Buffer Zones. *Journal of Wildlife Management* 74: 102–108.
- BURNHAM, K.P. and D.R. ANDERSON. 2002. *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*. Second Ed. Springer-Verlag, New York, New York, USA.
- CATLIN, D.H., J.H. FELIO and J.D. FRASER. 2011. Effect of great-horned owl trapping on chick survival in Piping Plovers. *Journal of Wildlife Management* 75: 458–462.
- . 2013. Effects of water discharge on fledging time, growth, and survival of Piping Plovers on the Missouri River. *Journal of Wildlife Management* 77: 525–533.
- CATLIN, D.H., O. MILENKAYA, K.L. HUNT, M.J. FRIEDRICH and J.D. FRASER. 2014. Can river management improve the Piping Plover's long-term survival on the Missouri River? *Biological Conservation* 180: 196–205.
- CHAMBERLAIN, M.J., B.D. LEOPOLD and L.M. CONNER. 2003. Space Use, Movements and Habitat Selection of Adult Bobcats (*Lynx rufus*) in Central Mississippi. *The American Midland Naturalist* 149: 395–405.
- COLWELL, M.A., S.J. HURLEY, J.N. HALL and S.J. DINSMORE. 2007. Age-related survival and behavior of Snowy Plover chicks. *Condor* 109: 638–647.
- DEROSE-WILSON, A.L., K.L. HUNT, J.D. MONK, D.H. CATLIN, S.M. KARPANTY and J.D. FRASER. 2018. Piping Plover Chick Survival Negatively Correlated With Beach

- Recreation. *The Journal of Wildlife Management* 82: 1608–1616.
- DINKINS, J.B., M.R. CONOVER, C.P. KIROL and J.L. BECK. 2012. Greater Sage-Grouse (*Centrocercus urophasianus*) select nest sites and brood sites away from avian predators. *The Auk* 129: 600–610.
- ELIAS, S.P., J.D. FRASER and P.A. BUCKLEY. 2000. Piping Plover Brood Foraging Ecology on New York Barrier Islands. *Journal of Wildlife Management* 64: 346–354.
- ELLIOTT-SMITH, E. and S.M. HAIG. 2004. Piping Plover (*Charadrius melodus*), Version 2.0. In: *The Birds of North America* online. (A.F. Poole, ed). Cornell Lab of Ornithology, Ithaca, NY, USA. <<https://birdsna.org/Species-Account/bna/species/pipplo>> (20 December 2018).
- FLEMMING, S.P., R.D. CHIASSON, P.C. SMITH, P.J. AUSTIN-SMITH and R.P. BANCROFT. 1988. Piping Plover Status in Nova Scotia Related to Its Reproductive and Behavioral Responses to Human Disturbance. *Journal of Field Ornithology* 59: 321–330.
- FRASER, J.D. AND D.H. CATLIN. 2019. Habitat ecology and conservation of Charadrius plovers. In: *Population Ecology and Conservation of Charadrius plovers. Studies in Avian Biology* (Colwell, M.A. and S.M. Haig, eds.), CRC Press. *In press*.
- GLOVER, H.K., M.A. WESTON, G.S. MAGUIRE, K.K. MILLER and B.A. CHRISTIE. 2011. Towards ecologically meaningful and socially acceptable buffers: Response distances of shorebirds in Victoria, Australia, to human disturbance. *Landscape and Urban Planning* 103: 326–334.
- GOLDIN, M.R. and J. V REGOSIN. 1998. Chick Behavior, Habitat Use, and Reproductive Success of Piping Plovers at Goosewing Beach, Rhode Island. *Journal of Field Ornithology* 69: 228–234.
- HAFFNER, C.D., F.J. CUTHBERT and T.W. ARNOLD. 2009. Space use by Great Lakes Piping Plovers during the breeding season. *Journal of Field Ornithology* 80: 270–279.
- HECHT, A. and S.M. MELVIN. 2009. Expenditures and Effort Associated With Recovery of Breeding Atlantic Coast Piping Plovers. *Journal of Wildlife Management* 73: 1099–

1107.

HIJMANS, R.J. 2017. Geosphere: Spherical Trigonometry. R package version 1.5–7.
<<https://CRAN.R-project.org/package=geosphere>> (07 December 2018).

HIXON, M.A. 1980. Food Production and Competitor Density as the Determinants of Feeding Territory Size. *The American Naturalist* 115: 510–530.

HUNT, K.L., J.D. FRASER, M.J. FRIEDRICH, S.M. KARPANTY and D.H. CATLIN. 2018. Demographic response of Piping Plovers suggests that engineered habitat restoration is no match for natural riverine processes. *The Condor: Ornithological Applications* 120: 149–165.

KNOFF, F.L. and J.R. RUPERT. 1996. Reproduction and Movements of Mountain Plovers Breeding in Colorado. *The Wilson Bulletin* 108: 28–35.

KOSZTOLÁNYI, A., T. SZÉKELY, I.C. CUTHILL, K.T. YILMAZ and S. BERBEROĞLU. 2006. Ecological constraints on breeding system evolution: The influence of habitat on brood desertion in Kentish plover. *Journal of Animal Ecology* 75: 257–265.

KOSZTOLÁNYI, A., T. SZÉKELY and I.C. CUTHILL. 2007. The function of habitat change during brood-rearing in the precocial Kentish plover *Charadrius alexandrinus*. *Acta Ethologica* 10: 73–79.

KRIJGSVELD, K.L., J.W.H. RENEERKENS, G.D. MCNETT and R.E. RICKLEFS. 2003a. Time Budgets and Body Temperatures of American Golden-Plover Chicks in Relation to Ambient Temperature. *Condor* 105: 268–278.

KRIJGSVELD, K.L., G.H. VISSER and S. DAAN. 2003b. Foraging behavior and physiological changes in precocial quail chicks in response to low temperatures. *Physiology and Behavior* 79: 311–319.

KUKLINKSKI, M.L., L.M. HOUGHTON and J.D. FRASER. 1996. Piping Plover Breeding Ecology on Cape Hatteras National Seashore with Special Reference to the Effect of Temperature on Productivity. Unpublished Report to the National Park Service.

Department of Fisheries and Wildlife Sciences, Virginia Polytechnic Institute and State University, Blacksburg, VA, USA.

- KWON, E., J.D. FRASER, D.H. CATLIN, S.M. KARPANTY, C.E. WEITHMAN and B. MUIZNIEKS. 2018. Presence of Ghost Crabs and Piping Plover Nesting Success. *Journal of Wildlife Management* 82: 850–856.
- LAING, K.K. and D.G. RAVELING. 1993. Habitat and Food Selection by Emperor Goose Goslings. *Condor* 95: 879–888.
- LE FER, D., J.D. FRASER and C.D. KRUSE. 2008a. Piping Plover Foraging-Site Selection on the Missouri River. *Waterbirds* 31: 587–592.
- . 2008b. Piping Plover Chick Foraging, Growth, and Survival in the Great Plains. *Journal of Wildlife Management* 72: 682–687.
- LOEGERING, J.P. and J.D. FRASER. 1995. Factors Affecting Piping Plover Chick Survival in Different Brood-rearing Habitats. *Journal of Wildlife Management* 59: 646–655.
- LOEGERING, J.P., J.D. FRASER and L.L. LOEGERING. 1995. Ghost Crab Preys on a Piping Plover Chick. *The Wilson Bulletin* 107: 768–769.
- MELVIN, S.M., C.R. GRIFFIN and L.H. MACIVOR. 1991. Recovery strategies for Piping Plovers in managed coastal landscapes. *Coastal Management* 19: 21–34.
- MELVIN, S.M., A. HECHT and C.R. GRIFFIN. 1994. Piping Plover Mortalities Caused by Off-Road Vehicles on Atlantic Coast Beaches. *Wildlife Society Bulletin* 22: 409–414.
- MELVIN, S.M., L.H. MACIVOR and C.R. GRIFFIN. 1992. Predator exclosures: A technique to reduce predation at Piping Plover nests. *Wildlife Society Bulletin* 20: 143–148.
- R CORE TEAM (2018). R: A Language and Environment for Statistical Computing. Version 3.5.2. R Foundation for Statistical Computing, Vienna, Austria. <<http://www.R-project.org>> (20 December 2018).
- REES, J.D., J.K. WEBB, M.S. CROWTHER and M. LETNIC. 2015. Carrion subsidies provided

- by fishermen increase predation of beach-nesting bird nests by facultative scavengers. *Animal Conservation* 18: 44–49.
- ROBINSON, S.G., J. FRASER, D. CATLIN, S. KARPANTY, J. ALTMAN, R. BOETTCHEER, K. HOLCOMB, C. HUBER, K. HUNT AND A. WILKE. Irruptions: evidence for breeding season habitat limitation in Piping Plovers. *Avian Conservation and Ecology. In review*
- RUTHRAUFF, D.R. and B.J. MCCAFFERY. 2005. Survival of Western Sandpiper broods on the Yukon-Kuskokwim Delta, Alaska. *Condor* 107: 597–604.
- SÆTHER, B.-E. and Ø. BAAKE. 2000. Avian Life History Variation and Contribution of Demographic Traits to the Population Growth Rate. *Ecology* 81: 642–653.
- SCHEKKERMAN, H. and A. BOELE. 2009. Chicks of the black-tailed godwit *Limosa limosa*: Vulnerability to weather and prey size. *Journal of Avian Biology* 40: 369–379.
- SCHEKKERMAN, H. and G.H. VISSER. 2001. Prefledging Energy Requirements in Shorebirds: Energetic Implications of Self-Feeding Precocial Development. *The Auk* 118: 944–957.
- SCHLACHER, T.A., L.K. CARRACHER, N. PORCH, R.M. CONNOLLY, A.D. OLDS, B.L. GILBY, ET AL. 2016. The Early Shorebird Will Catch Fewer Invertebrates on Trampled Sandy Beaches. *Plos One* 11: e0161905.
- SCHLACHER, T.A., T. NIELSEN and M.A. WESTON. 2013. Human recreation alters behaviour profiles of non-breeding birds on open-coast sandy shores. *Estuarine, Coastal and Shelf Science* 118: 31–42.
- SCHWEITZER, S.H. 2017. 2017 Breeding Season Report for the Piping Plover in North Carolina. Unpublished Report. North Carolina Wildlife Resource Commission. New Bern, NC.
- SIGNORELL, N., S. WIRTHNER, P. PATTHEY, R. SCHRANZ, L. ROTELLI and R. ARLETTAZ. 2010. Concealment from predators drives foraging habitat selection in brood-rearing Alpine black grouse *Tetrao tetrix* hens: habitat management implications. *Wildlife Biology* 16: 249–257.

- STARCK, J.M. and R.E. RICKLEFS. 1998. Patterns of Development: The Altricial-Precocial Spectrum. In: Avian Growth and Development: Evolution Within the Altricial-Precocial Spectrum (J.M. Starck & R.E. Ricklefs, eds.), pp. 3–30. Oxford University Press, New York, New York, USA.
- ST CLAIR, J.J.H., G.E. GARCÍA-PEÑA, R.W. WOODS and T. SZÉKELY. 2010. Presence of mammalian predators decreases tolerance to human disturbance in a breeding shorebird. *Behavioral Ecology* 21: 1285–1292.
- U.S. FISH AND WILDLIFE SERVICE. 1985. Determination of Endangered and Threatened Status for the Piping Plover. Final Rule. *Federal Register* 50: 50726–50734. USFWS, Washington, D.C., USA.
- . 1996. Piping Plover (*Charadrius melodus*), Atlantic Coast Population, Revised Recovery Plan. U.S. Fish and Wildlife Service. Hadley, Massachusetts.
- VITZ, A.C. and A.D. RODEWALD. 2010. Movements of Fledgling Ovenbirds (*Seiurus aurocapilla*) and Worm-eating Warblers (*Helmitheros vermivorum*) within and beyond the Natal Home Range. *The Auk* 127: 364–371.
- WALKER, K.M., J.D. FRASER, D.H. CATLIN, S.J. RITTER, S.G. ROBINSON, H.A. BELLMAN, ET AL. Hurricane Sandy and Engineered Human Response Created Habitat for a Threatened Species. *Ecosphere*. *In review*.
- WEITHMAN, C.E., S.G. ROBINSON, K.L. HUNT, J. ALTMAN, H.A. BELLMAN, A.L. DEROSE-WILSON, ET AL. Growth of Two Atlantic Coast Piping Plover Populations. *The Condor: Ornithological Applications*. *In review*.
- WESTON, M.A., F. DODGE, A. BUNCE, D.G. NIMMO and K.K. MILLER. 2012. Do temporary beach closures assist in the conservation of breeding shorebirds on recreational beaches? *Pacific Conservation Biology* 18: 47–55.
- WESTON, M.A. and M.A. ELGAR. 2005. Disturbance to brood-rearing Hooded Plover *Thinornis rubricollis*: responses and consequences. *Bird Conservation International* 15: 193–209.

- WILSON, C.A. and M.A. COLWELL. 2010. Movements and Fledging Success of Snowy Plover (*Charadrius alexandrinus*) Chicks. *Waterbirds* 33: 331–340.
- WILTERMUTH, M.T., M.J. ANTEAU, M.H. SHERFY and A.T. PEARSE. 2015. Habitat selection and movements of Piping Plover broods suggest a tradeoff between breeding stages. *Journal of Ornithology* 156: 999–1013.
- WOLCOTT, D.L. and T.G. WOLCOTT. 1999. High Mortality of Piping Plovers on Beaches with Abundant Ghost Crabs: Correlation, Not Causation. *The Wilson Bulletin* 111: 321–329.
- YASUÉ, M. 2006. Environmental factors and spatial scale influence shorebirds' responses to human disturbance. *Biological Conservation* 128: 47–54.

Table 1. Linear regression model variables, descriptions, and predicted effects on hourly movement rates of Piping Plover broods at Cape Hatteras National Seashore and Pea Island National Wildlife Refuge, North Carolina 2016–2017. Variables were collected during brood observations

Variable	Descriptions	Predicted effect on brood movement	Reasoning	Sources
Habitat ^a	Wet habitats (moist or saturated sand and mud)	Negative	Chicks would maximize their foraging opportunities by continuing to occupy moist foraging habitats and moving less, and more readily move in dry habitats.	Burger 1994, Goldin and Regosin 1998, Elias et al. 2000, Yasué 2006, Le Fer et al. 2008b
	Dry habitats (Dry or arid sand or shell substrates)	Positive		
Behavior ^b	Disturbed behavior (crouching, fleeing, direct encounters, chasing)	Positive	Larger movements after disturbed behavior as chicks avoid the disturbance	Flemming et al. 1988, Burger 1994, Goldin and Regosin 1998, Elias et al. 2000
	Undisturbed behavior (standing/sitting, running/walking, brooding, preening)	Negative	Smaller movements following undisturbed behavior, as chicks would not expend energy to move unless necessary	

	Foraging (pecking, probing)	Negative	Time spent foraging indicative of habitat quality, therefore, reduced movements at sites where chicks spend large amounts of time foraging	
	Other (wing stretching/flapping, scratching, swimming)	Negative	Other behaviors observed are typically non-mobile activities	
Brood age	Day 0–25 after hatch	Positive	Increased mobility with age; fleeing as age-related response to disturbance increases	Knopf and Rupert 1996, Ruthrauff and McCaffery 2005, Wilson and Colwell 2010
Potential disturbances ^c	Visible Ghost crabs	Positive	Chicks move to avoid high crab densities	Wolcott and Wolcott 1999, Elliott-Smith and Haig 2004,
	Non-parental plovers	Positive	Chicks move to avoid conspecific territorial adults	Colwell et al. 2007,
	Killdeer	Positive	Chicks move to avoid interspecific territorial interactions	DeRose-Wilson et al. 2018

	Potential or perceived avian predators (crows, gulls, osprey or other raptors, herons)	Negative	Chicks crouch and move less to avoid detection by avian predators	
	Human-related (pedestrians, vehicles, UTVs)	Positive	Chicks move to avoid mobile and stationary pedestrians and vehicles	
Forage rate	Foraging attempts per minute during observation period	Negative	Similar to time spent foraging, foraging rate represents potential interaction of age and habitat	Loefering and Fraser 1995, Goldin and Regosin 1998, Elias et al. 2000

^a Dominant habitat type within ~2m radius of focal chick during a behavior sample.

^b Proportion of time focal chick exhibits behaviors during observation sample.

^c Individuals per 100m² observed during point counts of potential disturbance sources within 500m of brood.

Table 2. Selection table for models describing daily Piping Plover brood movement at Cape Hatteras National Seashore and Pea Island National Wildlife Refuge, North Carolina 2015–2017.

Model ^a	K ^b	logLik ^c	ΔAICc	w _i ^d
Age	3	-180.51	0.00	0.31
Age + Age ²	4	-179.72	0.59	0.23
Age + Year	5	-179.06	1.50	0.15
Year	4	-180.21	1.58	0.14
Date	3	-181.66	2.29	0.10
Temperature + Precipitation	4	-180.92	3.01	0.07
Age + Year + Date + Temperature + Precipitation	8	-178.43	7.22	0.01

^a Model variables are defined as: age = the average age of a brood between two consecutive observations; Year = 2015 is the reference; Date = Julian date; Temperature = recorded maximum daily temperature; Precipitation = daily recorded rainfall amount.

^b Number of model parameters.

^c Log likelihood.

^d Model weight.

Table 3. Average proportion of time Piping Plover chicks spent exhibiting behaviors at Cape Hatteras National Seashore and Pea Island National Wildlife Refuge, North Carolina 2016–2017. Behaviors were instantaneously sampled every 10 seconds for 5 minutes from a randomly selected focal chick. Average, standard deviation (SD), and range over 68 observations used in movement analysis are presented.

Behavior ^a	Mean	SD	Minimum	Maximum
Disturbed	0.008	0.027	0.000	0.167
Undisturbed	0.808	0.131	0.500	1.000
Foraging	0.174	0.134	0.000	0.500
Other	0.005	0.010	0.000	0.050

^a Behaviors were categorized as follows: Disturbed = crouching, fleeing, chasing, direct encounters; Undisturbed = brooding, preening, standing/sitting, walking; Foraging = pecking, probing, drinking; Other = uncategorized behaviors (e.g., stretching, hop-flying).

Table 4. Density of potential disturbance sources (individuals/100m²) observed within 500m of focal brood during brood observation point counts at Cape Hatteras National Seashore and Pea Island National Wildlife Refuge, North Carolina, 2016–2017. Average, standard deviation (SD) and range over 68 observations used in movement analysis are presented.

Potential Disturbance Source	Average	SD	Minimum	Maximum
Bird ^a	0.006	0.007	0.000	0.067
Ghost Crabs	0.001	0.004	0.000	0.022
Human ^b	0.022	0.051	0.000	0.199
Killdeer	0.001	0.002	0.000	0.010
Plovers ^c	<0.001	0.001	0.000	0.003

^a Avian sources include potential and/or perceived avian predators (e.g., ospreys, gulls, crows, herons)

^b Human sources include pedestrians and vehicles.

^c Only adult plovers that were not the focal brood's parents were counted. Average value = 0.0002.

Table 5. Selection table for models describing environmental and behavior effects on Piping Plover hourly brood movement rate at Cape Hatteras National Seashore and Pea Island National Wildlife Refuge, North Carolina 2016–2017. Data from 2015 were excluded due to differences in sampling.

Model ^a	K ^b	logLik ^c	ΔAICc	w _i ^d
Age	3	-112.95	0.00	0.37
Age + wet habitat	4	-112.31	0.98	0.23
Age + Disturbed + Undisturbed + Other	6	-110.35	1.80	0.15
Age + ppm	4	-112.77	1.89	0.14
Age + wet habitat + Disturbed + Undisturbed + Other	7	-110.19	3.96	0.05
Age + ppm + Disturbed + Undisturbed + Other	7	-110.21	3.99	0.05
Age + PIPL + KILL + Avian + People + Crabs	8	-111.74	9.64	0.00
Age + wet habitat + PIPL + KILL + Avian + People + Crabs	9	-110.64	10.10	0.00
Age + ppm + PIPL + KILL + Avian + People + Crabs	9	-111.50	11.81	0.00
Age + ppm + wet habitat + PIPL + KILL + Avian + People + Crabs + Disturbed + Undisturbed + Other	14	-106.48	16.59	0.00

^a Model variables are defined as: age = maximum brood age at observation; wet habitat = binary variable of habitat type brood was observed in; ppm = foraging rate (pecks per minute); disturbed, undisturbed, other = proportion of time brood was observed exhibiting

behaviors; PIPL, KILL, AVIAN, PEOB, CRAB = individuals/100m² of each category observed within 500m of brood.

^b Number of model parameters.

^c Log likelihood.

^d Model weight.

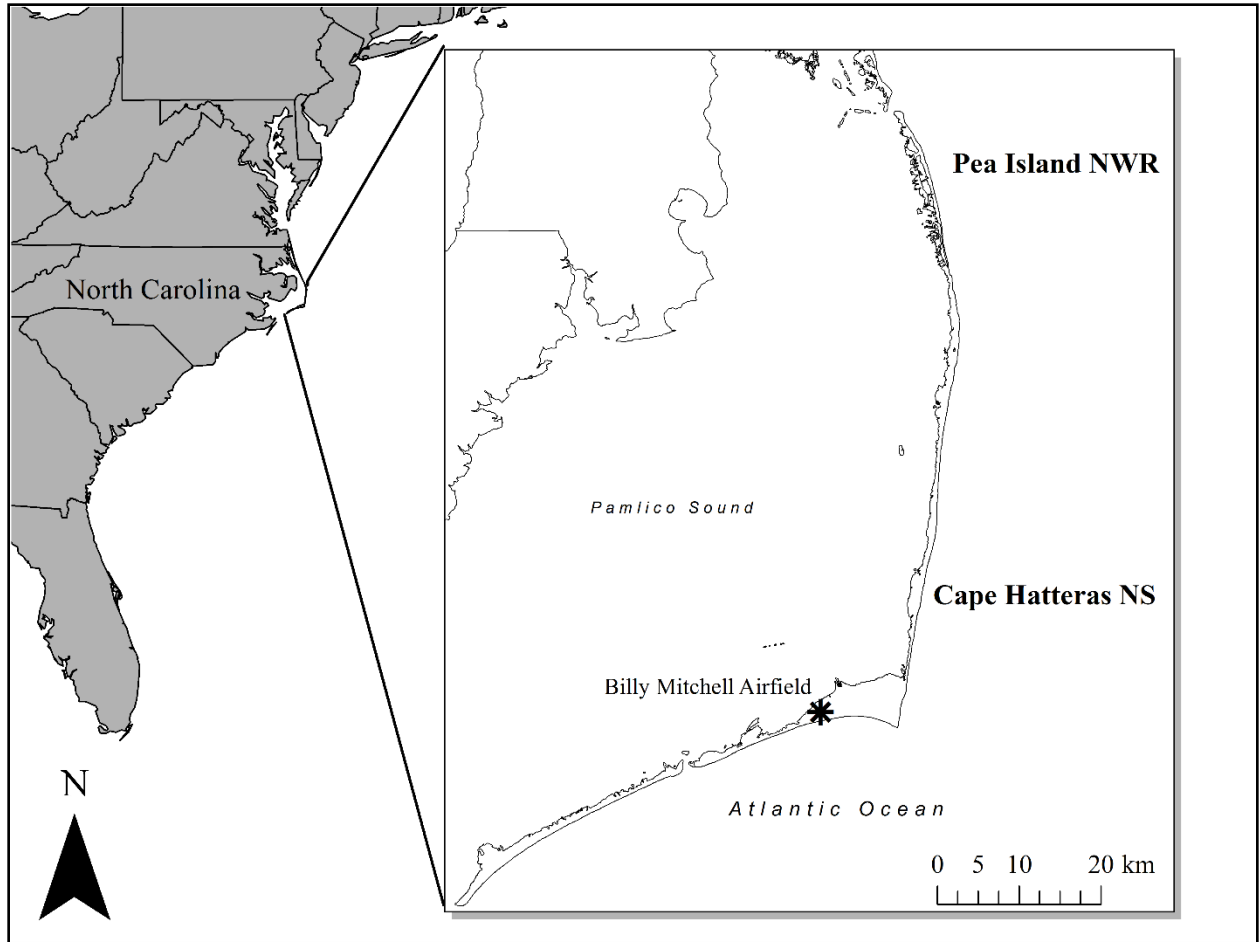


Fig. 1. Map of the study area in Cape Hatteras National Seashore and Pea Island National Wildlife Refuge in North Carolina, USA.

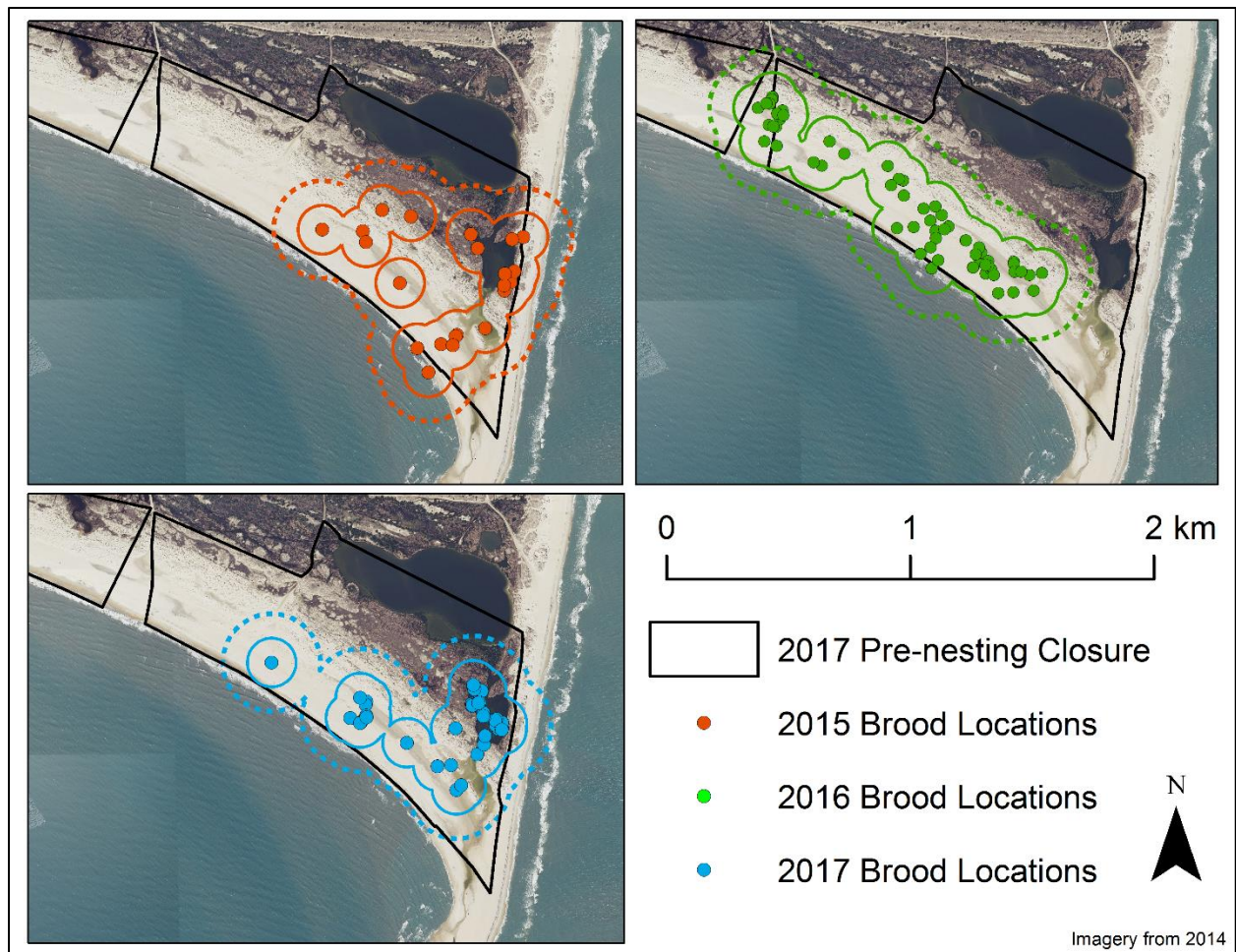


Fig. 2. Brood locations with pedestrian buffers (100m; solid lines) and small ORV buffers (200m; dashed lines) in reference to pre-nesting closure areas at Cape Point, a breeding area of Piping Plovers at Cape Hatteras National Seashore, 2015–2017. Pre-nesting closure shown is representative of pre-nesting closures at Cape Point in all years.

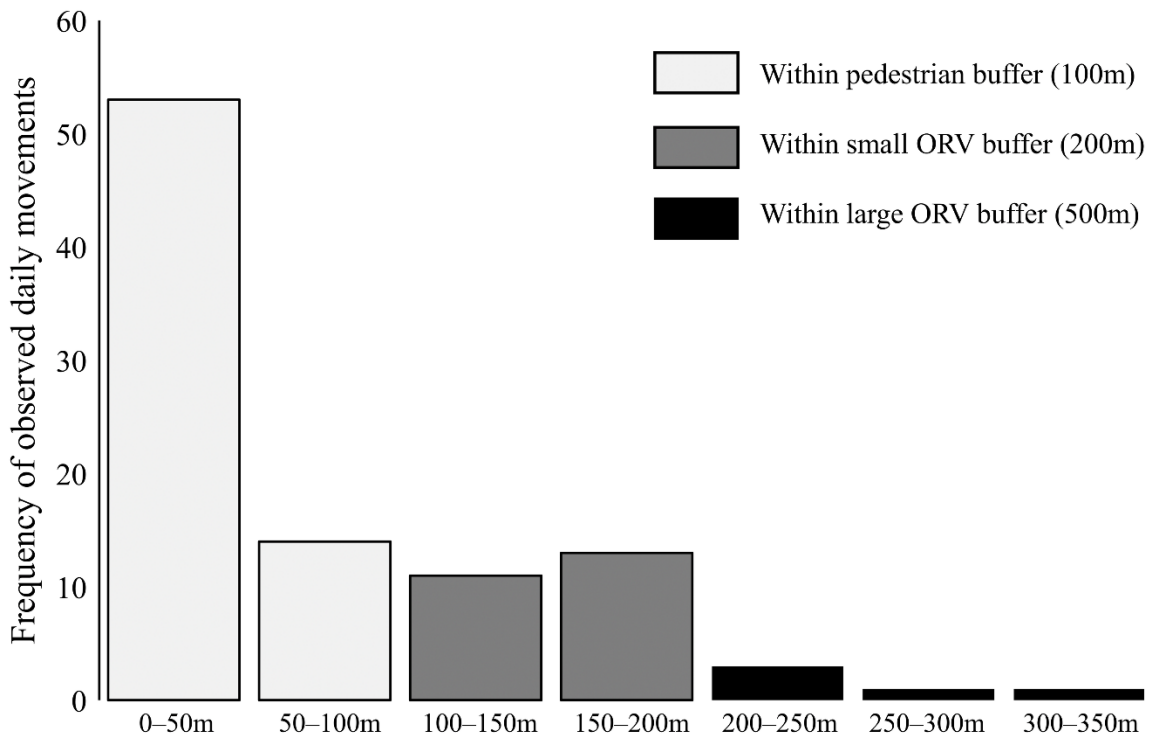


Fig. 3. Frequency of observed daily brood movements at Cape Hatteras National Seashore and Pea Island National Wildlife Refuge, North Carolina, 2015–2017. Movements are straight-line distances between consecutive observations of daily brood locations. Bar colors represent distance classes that were contained within current management buffer sizes used at Cape Hatteras National Seashore.

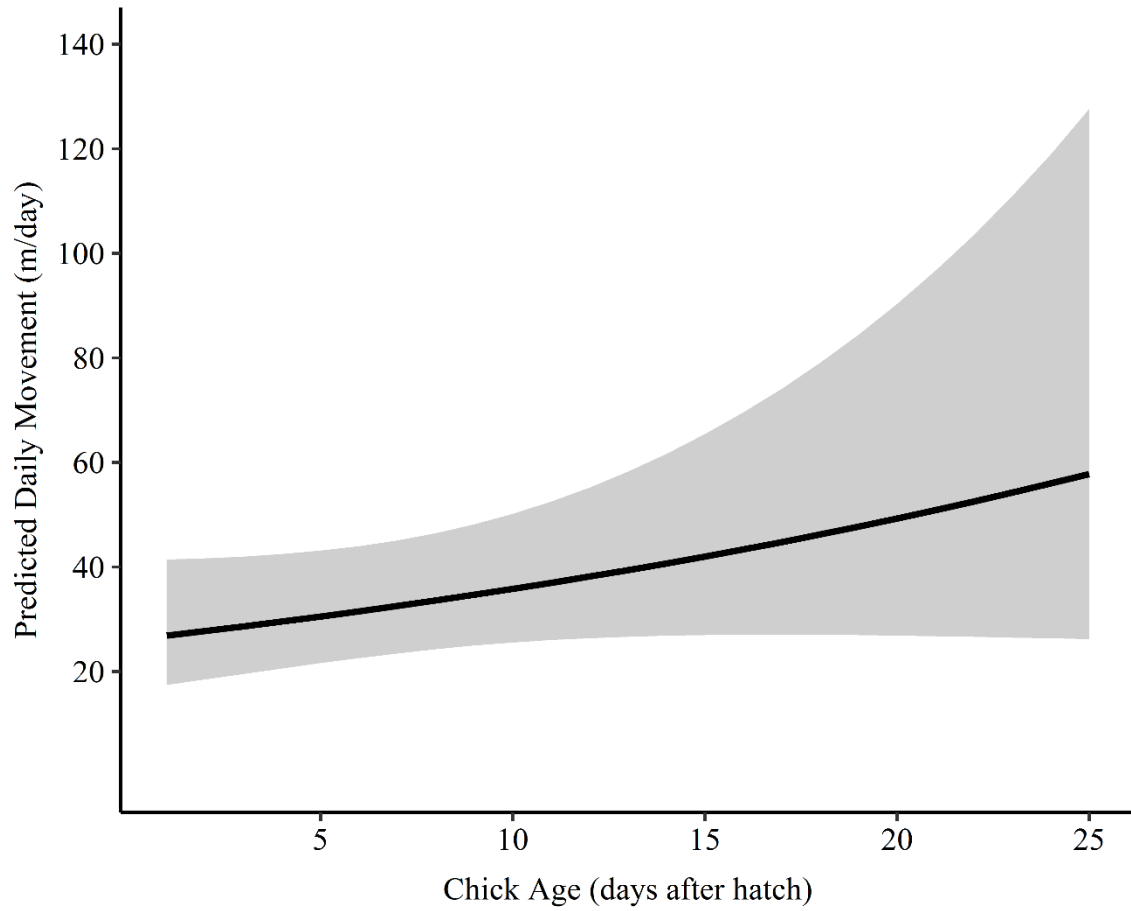


Fig. 4. Predicted daily Piping Plover brood movement during the pre-fledge period at Cape Hatteras National Seashore and Pea Island National Wildlife Refuge, North Carolina 2015–2017. Band represents 95% confidence interval.

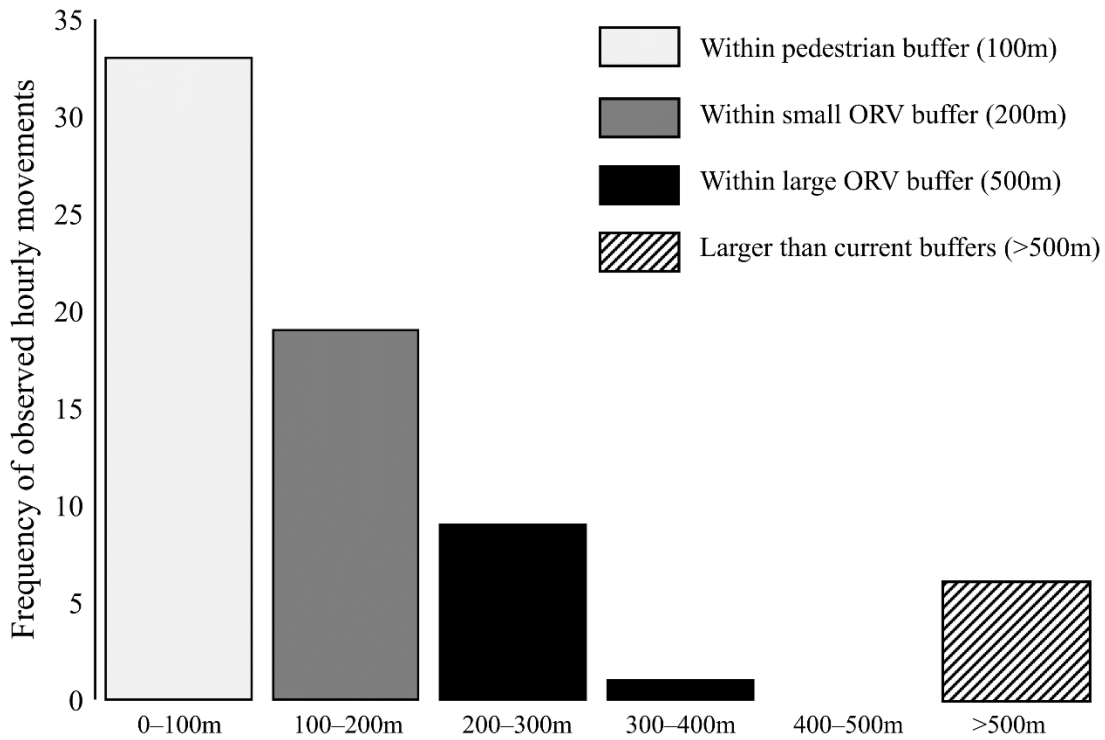


Fig. 5. Frequency of observed hourly brood movements under continuous observation at Cape Hatteras National Seashore and Pea Island National Wildlife Refuge, North Carolina, 2016–2017. Movements are straight-line distances between consecutive brood locations during continuous observation periods. Bar colors represent distance classes compared to current management buffer sizes used at Cape Hatteras National Seashore.

SUPPLEMENTAL MATERIAL

Table S1. Total counts of potential disturbance sources observed during brood observation periods at Cape Hatteras National Seashore and Pea Island National Wildlife Refuge, North Carolina, 2016–2017. Dashes indicate no potential disturbance counts were conducted.

Area ^a	Ghost Crabs	Killdeer	Plovers ^b	Human Sources ^c	Avian Sources ^d	<i>n</i> ^e
2016						
Cape Point ^f	10	0	0	108	277	32
Oregon Inlet USCG Station ^g	—	—	—	—	—	—
North Pond Area ^g	—	—	—	—	—	—
South Beach ^f	—	—	—	—	—	—
2017						
Cape Point	11	26	13	386	187	30
Oregon Inlet USCG Station	4	3	0	15	100	9
North Pond Area	0	14	0	701	26	15
South Beach	17	0	0	3	4	2

^a Commonly used names of areas of Piping Plover breeding activity.

^b Plovers that were not parents of the focal brood.

^c Includes vehicles and pedestrians.

^d Includes gulls, ospreys, and crows.

^e Number of potential disturbance count samples.

^f Area in Cape Hatteras National Seashore.

^g Area in Pea Island National Wildlife Refuge.

**CHAPTER 3: DISCOVERY OF AN IMPORTANT STOPOVER LOCATION FOR MIGRATORY
PIPING PLOVERS (*CHARADRIUS MELODUS*) ON SOUTH POINT, OCRACOKE ISLAND, NORTH
CAROLINA, USA**

Previously published in *Waterbirds*, Vol. 41, Issue 1, pages 56–62

**Discovery of an Important Stopover Location for Migratory Piping Plovers (*Charadrius
melodus*) on South Point, Ocracoke Island, North Carolina, USA**

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ABSTRACT.—Piping Plovers (*Charadrius melodus*) undertake comparatively short migrations for a shorebird and were not previously thought to congregate in large numbers during migration. Superpopulation size (individuals occurring at the study site during the study period) and stopover duration were estimated for migratory Piping Plovers on South Point, Ocracoke Island, North Carolina, USA, from 3 July–28 October 2016 by integrating a Jolly-Seber model and a binomial model of resighting and count data. We estimated 569 Piping Plovers (95% CI: 502–651) used South Point during fall migration in 2016, approximately 10% of the global population and approximately 15% of the Atlantic Coast population. Stopover duration differed between Piping Plovers that bred on or near our study site (Southern USA, 46 days, SD = 1.7) compared to individuals that bred in the northern area of the breeding range (Atlantic Canada, 41 days, SD = 2.0; New England States, USA, 44 days, SD = 1.8) and the central area of the breeding range (New York and New Jersey, USA, 26 days, SD = 1.4). South Point may be unique in that no other areas are known to host similar numbers of Piping Plovers during fall migration. *Received 14 September 2017, accepted 18 October 2017.*

Key words.—*Charadrius melodus*, conservation, endangered species, migration, Ocracoke, Piping Plover, shorebird, stopover duration.

Running Head: PIPING PLOVER MIGRATION STOPOVER

Piping Plovers (*Charadrius melodus*; hereafter, plovers) are small, temperate breeding shorebirds that are listed as endangered in Canada (Committee on the Status of Endangered Wildlife in Canada 2013) and are listed in the United States as endangered in the Great Lakes and as threatened elsewhere in the breeding range (U.S. Fish and Wildlife Service 1985). Plovers undertake short migrations (Range = 584–2,963 km; Gibson *et al.* unpubl. data) compared to other similar-sized shorebird species (e.g., Sanderlings (*Calidris alba*), Myers *et al.* 1985; Semipalmated Plovers (*C. semipalmatus*), Nol and Blanken 2014). Recent banding efforts throughout their range have allowed researchers to identify and locate individuals throughout the annual cycle (Gratto-Trevor *et al.* 2012, 2016; Catlin *et al.* 2015; Gibson *et al.* 2017), but data on their biannual migrations are still sparse. Although migration often comprises a short period of the life cycles of shorebirds, it may represent a disparate amount of physiological cost (Newton 2008). Additionally, use of few stopover sites by large proportions of a population may disproportionately affect that population (Weber *et al.* 1999; Runge *et al.* 2014). Comprehensive surveys have previously documented large groups of plovers during breeding and non-breeding seasons (Elliott-Smith *et al.* 2015), but plovers were not previously thought to congregate in large numbers during migration.

The goal of this study was to estimate the number of migrating plovers and their stopover duration at a presumed major stopover location on the Atlantic Coast of North America. We hypothesized that stopover duration would vary among distinct breeding groups along the Atlantic Coast in Canada and the USA (U.S. Fish and Wildlife Service 1996) and would be related to distance traveled to the study site from the breeding grounds.

METHODS

Study Area

We conducted surveys on South Point, Ocracoke Island, North Carolina, USA (35° 4' 21.20" N, 76° 0' 22.17" W; Fig. 1) from 3 July–28 October 2016. South Point is a barrier island spit, with a sandy ocean foreshore and backshore, sparsely to heavily vegetated dunes, and low-energy mud-, sand-, and algal flats that are covered by tides from the island's sound side. South Point is the eastern boundary of Ocracoke Inlet, separating Cape Hatteras and Cape Lookout National Seashores.

During the 2016 breeding season, the site was used by nesting plovers, American Oystercatchers (*Haematopus palliatus*), Least Terns (*Sternula antillarum*), Gull-billed Terns (*Gelochelidon nilotica*), Black Skimmers (*Rhynchops nigra*), and Wilson's Plovers (*C. wilsonia*). There were three Piping Plover nests from two pairs during the 2016 breeding season. All breeding attempts by plovers at South Point ended in the first week of July, and other plovers were seen on South Point after they were known or assumed to have finished breeding. There are few reports on specifically how many plovers use South Point during the winter, but a small number (< 50) of plovers overwinter in North Carolina (Cohen *et al.* 2008, Elliott-Smith *et al.* 2015).

Field Methods

We conducted plover abundance and resighting surveys approximately twice per week from 3 July–15 August 2016, approximately once per week from 16 August–30 September 2016, and approximately once every 2 weeks from 1 October–28 October 2016. Plovers were marked during numerous studies away from our site or before the study period began (Gratto-Trevor *et al.* 2012; Saunders *et al.* 2012; Stantial 2014; Carey *et al.* 2017). We

recorded all band combinations and counted the number of banded and unbanded birds using spotting scopes. We avoided double-counting individuals by ensuring we passed an individual before counting it and through communication among observers. We surveyed irrespective of tidal stage and in all weather conditions except continuous rain or when wind was blowing sand across the study area (> 30 kmph).

Analytical Methods

We estimated the probabilities of entering and remaining on South Point, the average stopover duration for an individual plover at South Point, and the number of individuals that stopped over at South Point. We used: 1) resighting of previously banded individuals; and 2) counts of banded and unbanded individuals observed during the fall migration of 2016. We used the Jolly-Seber superpopulation model (Kéry and Schaub 2012; Lyons *et al.* 2016) to estimate probabilities of initially entering (b) and remaining and surviving (persistence; φ) in the population. Additionally, we derived an estimate of stopover duration (\hat{S} , time between an individual's estimated arrival and departure) from the probabilities of entering (b) and leaving ($1-\varphi$) the observable population. This model also integrates a binomial model into the likelihood that uses count data of banded and unbanded individuals to estimate the proportion of the population that is marked to derive an estimate of the superpopulation size (N , total number of individuals available to be sampled at the study site during the study period; Schwarz and Arnason 1996) from the estimated number of marked birds that entered our study system (Lyons *et al.* 2016). Each individual-based encounter history represented the observation of an individual or lack thereof during each survey occasion, coinciding with counts of banded and unbanded birds. We included all plovers that were observed on surveys with unique band or flag

combinations in our capture histories. If birds were banded with non-unique combinations or marks, they were treated like unbanded individuals.

We assessed whether plovers from distinct breeding areas used South Point differently as a stopover site. We estimated persistence (φ) independently for individuals associated with five geographically distinct breeding sites (s): Atlantic Canada (CAN), New England States (Maine, New Hampshire, Massachusetts, Rhode Island, and Connecticut, USA; NEUS), New York and New Jersey, USA (NYNJ), Southern USA (Delaware, Maryland, Virginia and North Carolina, USA; SOUS), and non-Atlantic locations (Great Lakes and Great Plains populations; GLGP; U.S. Fish and Wildlife Service 1996). Although the Great Lakes and Great Plains breeding populations are geographically and demographically disparate from each other (Haig and Oring 1988), the number of observed individuals from these populations on South Point were too few (two and one individuals, respectively) to estimate independently. We assumed that detection probabilities (p) on South Point were identical for individuals associated with each breeding group. We included a random effect (ε) of survey occasion for both φ and p to account for the residual temporal (t) variation in each demographic rate.

$$\text{logit}(\varphi_{s,t}) = \bar{\varphi}_s + \varepsilon_{\varphi_t}$$

$$\varepsilon_{\varphi_t} \sim \text{normal}(0, \tau_\varphi)$$

$$\tau_\varphi = \sigma_\varphi^{-2}$$

$$\sigma_\varphi \sim \text{uniform}(0,20)$$

$$\bar{\varphi}_s \sim \text{uniform}(-20,20)$$

$$\text{logit}(p_t) = p_0 + \varepsilon_{p_t}$$

$$\varepsilon_{p_t} \sim \text{normal}(0, \tau_p)$$

$$\tau_p = \sigma_p^{-2}$$

$$\sigma_p \sim \text{uniform}(0,20)$$

$$p_0 \sim \text{uniform}(-20,20)$$

We constrained the banded proportion of the population (π) to be constant over the study period and drawn from a uniform distribution.

$$\pi \sim \text{uniform}(0,1)$$

As we allowed φ to vary among individuals associated with each breeding group, we also derived breeding group specific \hat{S} values to assess whether individuals from certain breeding areas used South Point for longer periods than others. Lastly, we followed model guidelines presented in Kéry and Schaub (2012) and 1) added augmented data to fix the parameter space to a known value (PX-DA; Royle and Dorazio 2012); and 2) specified entry (b) probabilities to be drawn from a Dirichlet prior. We augmented our observed capture histories with all-zero encounters ($n' = 300$) to account for individuals that may have been present but remained undetected (Royle and Dorazio 2012). We fixed the entry parameters for the last two occasions to 0 to assist with parameter convergence. We did not observe any new banded individuals in the last two occasions, indicating that few if any individuals were entering our study area at that time.

We assessed parameter convergence by visually examining chain convergence and using the Brooks-Gelman-Rubin criterion (\hat{R}) (Gelman and Rubin 1992; Brooks and Gelman 1998). We considered models with \hat{R} values < 1.1 at each parameter node to have converged. We specified our model in statistical program R (R Development Core Team 2016) using the package jagsUI (Kellner 2016) to call JAGS (Plummer 2016) and export model results back to program R. Model runs consisted of three chains with an adapt phase

of 15,000 iterations, followed by a burn-in period of 500 iterations; the posterior distribution was drawn by taking the 6th iteration from the next 45,000 iterations. All values are presented as mean \pm 1 SD unless otherwise noted.

RESULTS

We conducted 22 surveys from 3 July–28 October 2016. Mean time between surveys was 5.6 ± 3.6 days (Range = 2–15 days). We observed 78 uniquely banded plovers, and we observed a mean of 130 ± 68 birds (Range = 4–259) per survey and a mean of 21 ± 11 banded birds (Range = 0–40) per survey. The estimated proportion of the population that was marked (π) was 0.16 (95% CI: 0.15–0.17).

The estimated superpopulation size for the study period was 569 individuals (95% CI: 502–651), with a peak survey-specific estimate of 292 individuals (95% CI: 253–338) on 1 August 2016 (Fig. 2). Mean daily persistence varied among breeding groups (Table 1). NYNJ birds had the most variability in daily persistence, whereas SOUS birds had the least variability (in terms of SD; Table 1). Mean stopover duration also varied by breeding group. Birds from SOUS stayed the longest on South Point (46 days), but had similar stopover durations as those from the northern extent of the Atlantic Coast breeding range (CAN and NEUS; Table 1). Birds from the central Atlantic Coast breeding range (NYNJ) had much shorter stopovers (26 days). Due to the small number of GLGP individuals ($n = 3$), model parameters for this group were inestimable, thus we do not report them here.

DISCUSSION

South Point provided an important stopover location for an imperiled shorebird. The group of plovers that migrated through South Point in 2016 represents 14.7% of the Atlantic Coast breeding population (U.S. Fish and Wildlife Service 2017), and 9.9% of the global breeding population (Elliott-Smith *et al.* 2015). Additionally, our peak estimate suggests that 7.5% of the Atlantic Coast population (U.S. Fish and Wildlife Service 2017) was present on South Point in a single day. Although we encountered individuals from all three major breeding populations, nearly all (> 96%) banded individuals were known Atlantic Coast breeders, and we assumed that this was representative of the breeding locations of unbanded individuals. We are unaware of any other area that supports a similar number of plovers during migration. With such a large proportion of Atlantic Coast plovers using South Point, the site is reminiscent of other important stopover locations such as the Delaware Bay for Red Knots (Niles *et al.* 2008) and the Yellow Sea for Bar-tailed Godwits (*Limosa lapponica*), Grey Plovers (*Pluvialis squatarola*), and other shorebird species (Barter and Riegen 2004), where large portions of populations occur during migration.

Our study focused on fall migration for a single year (2016) on one side of an inlet; however, given high levels of site fidelity on the breeding (Catlin *et al.* 2015) and wintering (Gratto-Trevor *et al.* 2012) grounds, plovers may maintain high levels of site fidelity to migratory stopover locations (Smith and Houghton 1984). This fidelity suggests that while abundance estimates and timing of peak migration may vary, South Point annually hosts a substantial proportion of this species. In addition, Portsmouth Island, only 3 km across Ocracoke Inlet (Fig. 1), is geographically similar to South Point, offering similar habitat to migrating plovers. We observed movement of marked birds between these sites during

stopover periods, and Portsmouth Island may support additional migrating plovers that do not use South Point (Elliott-Smith and Haig 2004).

Site-specific abundance estimates of plovers have previously been conducted at midpoints of the breeding and winter periods, where individual dispersal is assumed to be rare (Elliott-Smith *et al.* 2015), but quantifying the number of migratory individuals is more challenging, as accounting for arrival and departure of unmarked individuals is difficult. Hence, this is the first estimate of a migratory population of plovers that explicitly accounts for movements of individuals into and out of the study area.

We observed a first peak in migration in late July, with a second peak in late September, suggesting that migration timing was bimodal. This later peak may be driven by the later migration of hatch-year individuals (Butler *et al.* 1987) and later migrating adults (Colwell 2010). However, weather events in 2016 may also have affected migration patterns. Hurricane Matthew passed near South Point on 9 October 2016 as a Category 1 storm (Stewart 2017), causing much of South Point to flood, resulting in temporary loss of usable habitat. After Hurricane Matthew, the estimated population dropped substantially (Fig. 2). Based on subsequent reports of banded individuals, we do not believe the decrease in numbers at South Point following Hurricane Matthew was due to mortality, but may have been due in part to birds leaving our site using a tail-wind (Ma *et al.* 2011) associated with the storm.

Stopover duration was not linearly related to distance from breeding area. Instead, it is possible that longer stopover duration on South Point was correlated with farther flights after departure (Lislevand *et al.* 2016). Unfortunately, we did not have data on subsequent stopover locations and wintering destinations for most individuals in the study. Future

studies of plover stopover duration should endeavor to link stopover locations with both breeding and wintering locations, but lower detection rates in the winter (Elliot-Smith *et al.* 2015) may complicate these attempts.

The plovers using South Point in 2016 were the largest group of plovers ever detected during migration. Use of this site for nearly a month or more suggests that South Point is a key stopover site for the species. Given the large proportion of this species that may use this site annually, conditions at South Point during key stopover periods may have widespread effects on population dynamics of the Atlantic Coast population (Weber *et al.* 1999). Further research should strive to identify if there are other important stopover sites for Piping Plovers and to evaluate the effects of these sites on stopover ecology and rangewide population dynamics.

ACKNOWLEDGMENTS

Funding for this study was provided by the National Park Service. We thank the National Park Service, the U.S. Fish and Wildlife Service, and the North Carolina Wildlife Resources Commission for support during this project. We thank C. Gratto-Trevor, P. Loring, P. Paton, M. Stantial, and A. Van Zoeren for their communication regarding banded birds observed during this study. We also thank S. Ritter for help with GIS data. We are grateful to the two anonymous reviewers whose comments improved the manuscript. Work was completed under U.S. Geological Survey Federal Bird Banding permit #21446, U.S. Fish and Wildlife Service Endangered Species permit #TE-103272-3, North Carolina Wildlife Resources Commission Endangered Species permit #16-ES00438, U.S. Department of the Interior Scientific Research and Collection permit #CAHA-2016-SCI-

0003, and Institutional Animal Care and Use Committee protocol #16-244. All applicable ethical guidelines for the use of birds in research have been followed, including those presented in the Ornithological Council's "Guidelines to the Use of Wild Birds in Research" (Fair *et al.* 2010).

LITERATURE CITED

- Barter, M. and A. Riegen. 2004. Northward shorebird migration through Yalu Jian National Nature Reserve. *Stilt* 46: 9–14.
- Brooks, S. P. and A. Gelman. 1998. General methods for monitoring convergence of iterative simulations. *Journal of Computational and Graphical Statistics* 7: 434–455.
- Butler, R. W., G. W. Kaiser and G. E. J. Smith. 1987. Migration chronology, length of stay, sex ratio, and weight of western sandpipers, (*Calidris mauri*) on the south coast of British Columbia. *Journal of Field Ornithology* 58: 103–111.
- Carey, A. M., K. Miles, S. G. Robinson, K. M. Walker, E. Kwon, J. D. Monk, H. A. Bellman, A. DeRose-Wilson, K. L. Hunt, J. D. Fraser and others. 2017. Multiple factor analysis of Piping Plovers and other beach-dependent species habitat use and population dynamics following storm and human created changes to barrier island habitats within the Fire Island National Seashore. Unpublished report, Virginia Tech, Department of Fish and Wildlife Conservation, Blacksburg, Virginia.
- Catlin, D. H., J. D. Fraser and J. H. Felio. 2015. Demographic responses of Piping Plovers to habitat creation on the Missouri River. *Wildlife Monographs* 192: 1–42.
- Cohen, J. B., S. M. Karpanty, D. H. Catlin, J. D. Fraser and R. A. Fischer. 2008. Winter ecology of Piping Plovers at Oregon Inlet, North Carolina. *Waterbirds* 31: 472–479.

- Colwell, M. A. 2010. Shorebird ecology, conservation, and management. University of California Press, Berkeley, California.
- Committee on the Status of Endangered Wildlife in Canada (COSEWIC). 2013. Assessment and status report on the Piping Plover *Charadrius melodus* in Canada. Unpublished report, COSEWIC, Ottawa, Ontario. http://www.registrelep-sararegistry.gc.ca/virtual_sara/files/cosewic/sr_Piping%20Plover_2013_e.pdf, accessed 7 August 2017.
- Elliott-Smith, E. and S. M. Haig. 2004. Piping Plover (*Charadrius melodus*), v. 2.0. No. 002 in The Birds of North America Online (P. G. Rodewald, Ed.). Cornell Lab of Ornithology, Ithaca, New York. <https://birdsna.org/Species-Account/bna/species/pipplo>, accessed 25 August 2017.
- Elliott-Smith, E., M. Bidwell, A. E. Holland and S. M. Haig. 2015. Data from the 2011 international Piping Plover census. Data Series 922, U.S. Department of the Interior, Geological Survey, Reston, Virginia. <https://pubs.usgs.gov/ds/0922/pdf/ds922.pdf>, accessed 1 March 2017.
- Fair, J., E. Paul and J. Jones (Eds.). 2010. Guidelines to the use of wild birds in research. Ornithological Council, Washington, D.C.
- Gelman, A. and D. B. Rubin. 1992. Inference from iterative simulation using multiple sequences. *Statistical Science* 7: 457–472.
- Gibson, D., D. H. Catlin, K. L. Hunt, J. D. Fraser, S. M. Karpanty, M. J. Friedrich, M. K. Bimbi, J. B. Cohen and S. B. Maddock. 2017. Evaluating the impact of man-made disasters on imperiled species: Piping Plovers and the Deepwater Horizon oil spill. *Biological Conservation* 212: 48–62.

- Gratto-Trevor, C., S. M. Haig, M. P. Miller, T. D. Mullins, S. Maddock, E. Roche and P. Moore. 2016. Breeding sites and winter site fidelity of Piping Plovers wintering in The Bahamas, a previously unknown major wintering area. *Journal of Field Ornithology* 87: 29–41.
- Gratto-Trevor, C., D. Amirault-Langlais, D. Catlin, F. Cuthbert, J. Fraser, S. Maddock, E. Roche and F. Shaffer. 2012. Connectivity in Piping Plovers: do breeding populations have distinct winter distributions? *Journal of Wildlife Management* 76: 348–355.
- Haig, S. M. and L. W. Oring. 1988. Distribution and dispersal in the Piping Plover. *Auk* 105: 630–638.
- Kellner, K. 2016. jagsUI: a wrapper around “rjags” to streamline “JAGS” analyses v. 1.4.4. R Foundation for Statistical Computing, Vienna, Austria. <https://cran.r-project.org/package=jagsUI>, accessed 10 November 2016.
- Kéry, M. and M. Schaub. 2012. Bayesian population analysis using WinBUGS: a hierarchical perspective, 1st ed. Academic Press, Waltham, Massachusetts.
- Lislevand, T., M. Briedis, O. Heggøy and S. Hahn. 2016. Seasonal migration strategies of Common Ringed Plovers *Charadrius hiaticula*. *Ibis* 159: 225–229.
- Lyons, J. E., W. L. Kendall, J. A. Royle, S. J. Converse, B. A. Andres and J. B. Buchanan. 2016. Population size and stopover duration estimation using mark-resight data and Bayesian analysis of a superpopulation model. *Biometrics* 72: 262–271.
- Ma, Z., N. Hua, X. Zhang, H. Guo, B. Zhao, Q. Ma, W. Xue and C. Tang. 2011. Wind conditions affect stopover decisions and fuel stores of shorebirds migrating through the south Yellow Sea. *Ibis* 153: 755–767.

- Myers, J. P., J. L. Maron and M. Sallaberry. 1985. Going to extremes: why do sanderlings migrate to the neotropics? *Ornithological Monographs* 36: 520–535.
- Newton, I. 2008. *The migration ecology of birds*. Elsevier, London, U.K.
- Niles, L. J., H. P. Sitters, A. D. Dey, P. W. Atkinson, A. J. Baker, K. A. Bennett, R. Carmona, K. E. Clark, N. A. Clark, C. Espoz and others. 2008. Status of the Red Knot (*Calidris canutus rufa*) in the Western Hemisphere. *Studies in Avian Biology* 36: 1–185.
- Nol, E. and M. S. Blanken. 2014. Semipalmated Plover (*Charadrius semipalmatus*) v. 2.0. No. 444 in *The Birds of North America Online* (P. G. Rodewald, Ed.). Cornell Lab of Ornithology, Ithaca, New York. <https://birdsna.org/Species-Account/bna/species/sempl>, accessed 27 October 2017.
- Plummer, M. 2016. JAGS: a program for analysis of Bayesian graphical models using Gibbs sampling v. 4.2.0. <http://mcmc-jags.sourceforge.net>, accessed 10 November 2016.
- R Development Core Team. 2016. R: a language and environment for statistical computing v. 3.3.2. R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org/>, accessed 5 November 2016.
- Royle, J. A. and R. M. Dorazio. 2012. Parameter-expanded data augmentation for Bayesian analysis of capture-recapture models. *Journal of Ornithology* 152: 521–537.
- Runge, C. A., T. G. Martin, H. P. Possingham, S. G. Willis and R. A. Fuller. 2014. Conserving mobile species. *Frontiers in Ecology and the Environment* 12: 395–402.
- Saunders, S. P., E. A. Roche, T. W. Arnold and F. J. Cuthbert. 2012. Female site familiarity increases fledging success in Piping Plovers (*Charadrius melodus*). *Auk* 129: 329–337.

- Schwarz, C. J. and A. N. Arnason. 1996. A general methodology for the analysis of capture-recapture experiments in open populations. *Biometrics* 52: 860–873.
- Smith, P. W. and N. T. Houghton. 1984. Fidelity of Semipalmated Plovers to a migration stopover area. *Journal of Field Ornithology* 55: 247–249.
- Stantial, M. L. 2014. Flight behavior of breeding Piping Plovers: implications for risk of collision with wind turbines. M.S. Thesis, State University of New York, Syracuse.
- Stewart, S. R. 2017. National Hurricane Center tropical cyclone report: Hurricane Matthew (AL142016) 28 September - 9 October 2016. U.S. Department of Commerce, National Oceanic and Atmospheric Administration, National Hurricane Center, Miami, Florida. http://www.nhc.noaa.gov/data/tcr/AL142016_Matthew.pdf, accessed 22 August 2017.
- U.S. Fish and Wildlife Service. 1985. Determination of endangered and threatened status for the Piping Plover. *Federal Register* 50: 50726–50734.
- U.S. Fish and Wildlife Service. 1996. Piping Plover (*Charadrius melodus*), Atlantic Coast population, revised recovery plan. U.S. Department of the Interior, Fish and Wildlife Service, Hadley, Massachusetts.
- <https://www.fws.gov/northeast/pipingplover/pdf/summary.pdf>, accessed 9 December 2014.
- U.S. Fish and Wildlife Service. 2017. Abundance and productivity estimates – 2016 update: Atlantic Coast Piping Plover population. U.S. Department of the Interior, Fish and Wildlife Service, Hadley, Massachusetts.
- https://www.fws.gov/northeast/pipingplover/pdf/Abundance_Productivity_2016_Update_final.pdf, accessed 1 November 2017.

Weber, T. P., A. I. Houston and B. J. Ens. 1999. Consequences of habitat loss at migratory stopover sites: a theoretical investigation. *Journal of Avian Biology* 30: 416–426.

Table 1. Parameter estimates for mean daily persistence rate (φ) and stopover duration (\hat{S}) for Piping Plovers at South Point, Ocracoke Island, North Carolina, USA. Persistence rate is the probability of surviving and remaining at South Point. Stopover duration is measured in days. Groups are based on previously defined breeding regions (U.S. Fish and Wildlife Service 1996).

Group	φ			\hat{S}		
	Mean	SD	95% CI	Mean	SD	95% CI
Atlantic Canada	0.958	0.038	0.859–0.999	41.4	2.0	37.9–45.8
New England, USA ^a	0.962	0.035	0.872–0.999	44.3	1.8	41.4–48.5
New York and New Jersey, USA	0.922	0.063	0.767–0.998	25.9	1.4	23.4–28.9
Southern USA ^b	0.971	0.026	0.905–0.999	46.1	1.7	43.5–49.9

^aNew England = Maine, New Hampshire, Massachusetts, Rhode Island, and Connecticut.

^bSouthern USA = Delaware, Maryland, Virginia, and North Carolina.

FIGURE CAPTIONS

Figure 1. Map of study site on South Point, Ocracoke Island, in relation to Ocracoke Inlet and Portsmouth Island, North Carolina, USA.

Figure 2. Estimated population size of migrating Piping Plovers on South Point, Ocracoke Island, North Carolina, USA, during migration resighting surveys in 2016. Error bars represent 95% Bayesian credible intervals.

Figure 1.

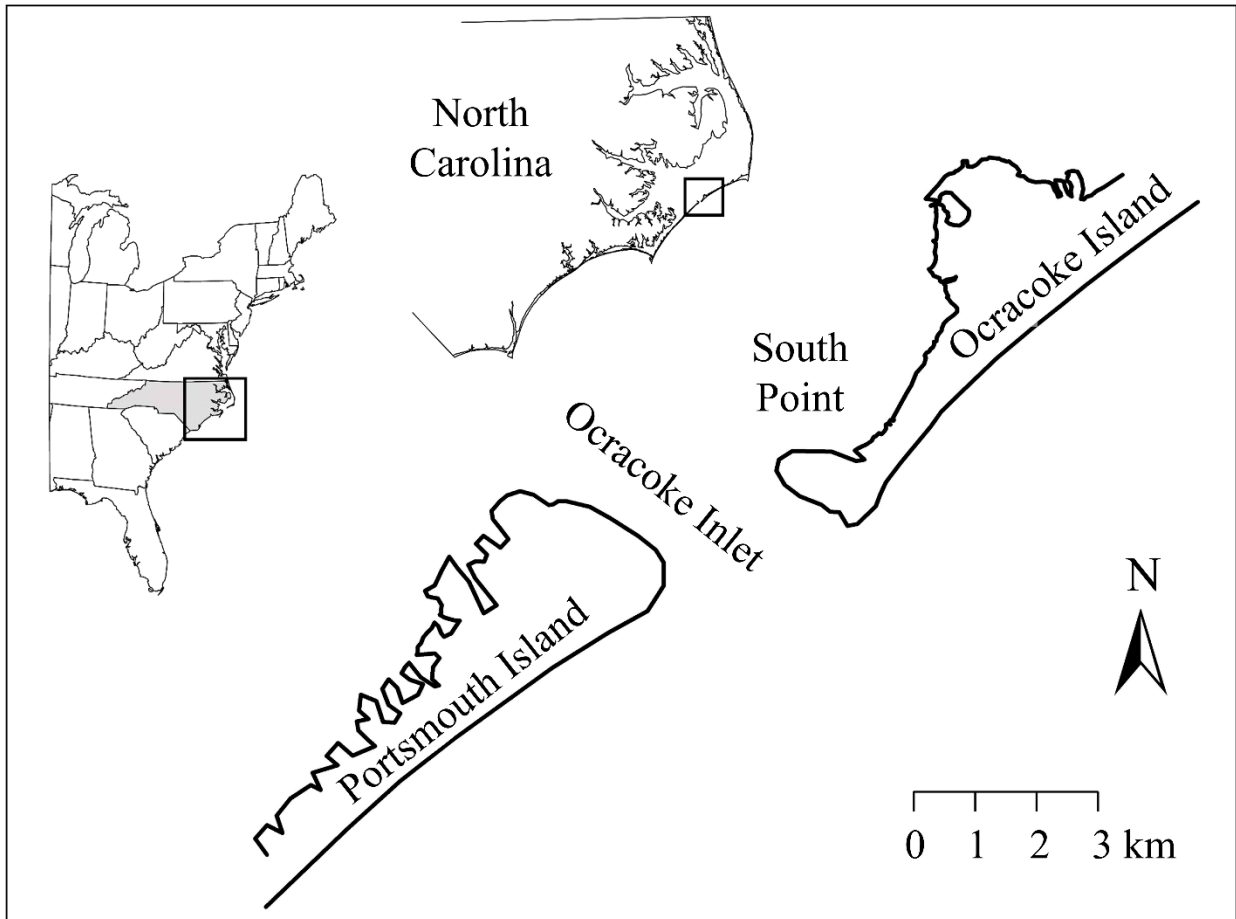
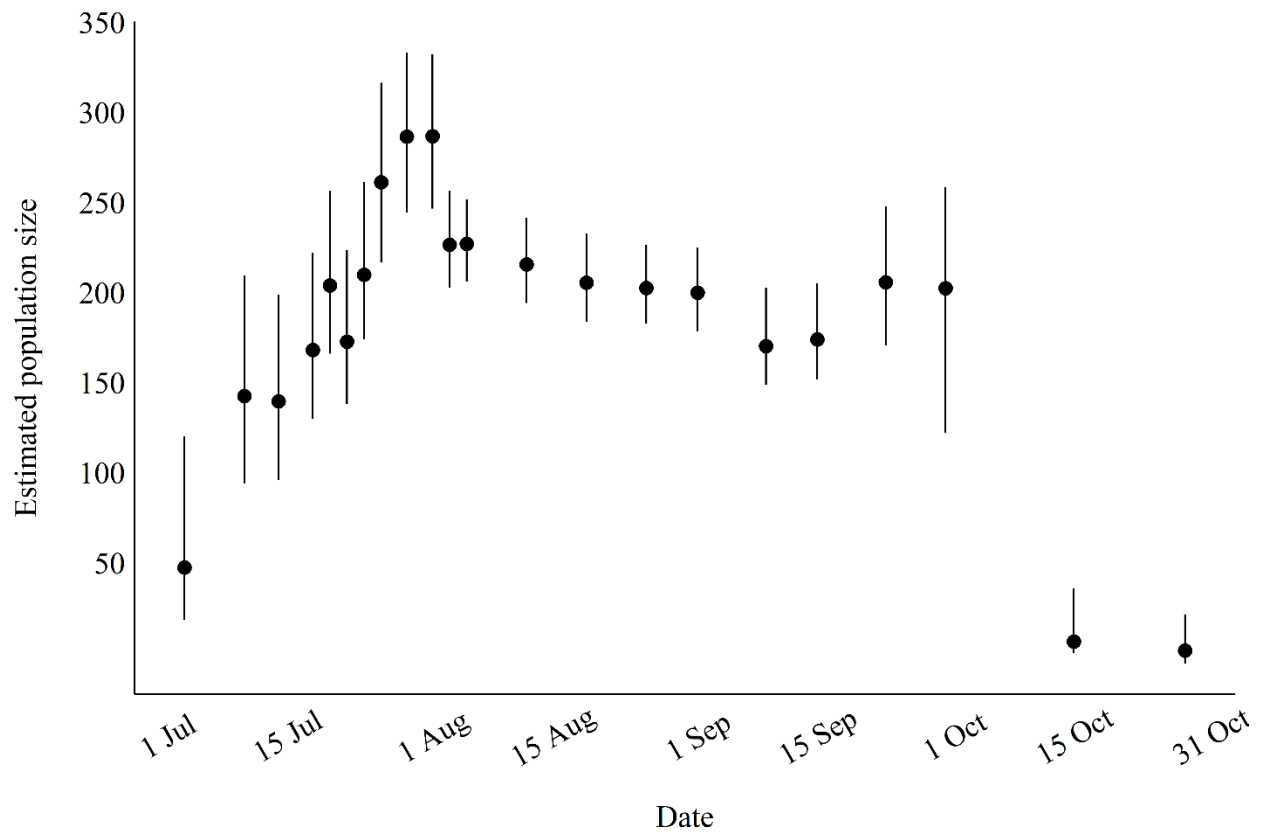


Figure 2.



CONCLUSIONS

During the breeding season, we found evidence that the small North Carolina population of federally Threatened Piping Plovers (*Charadrius melodus*; hereafter, 'plover') was in decline, based on several demographic rates. Compared to a plover population on Fire Island, NY, survival rates in North Carolina were similar for adults and in some years for juveniles, and similar to survival estimates in previous studies (Cohen et al. 2006, LeDee et al. 2010, Catlin et al. 2015). Based on long-term population and reproductive output estimates, we hypothesized that plovers in North Carolina may have higher survival rates than other areas on the Atlantic Coast (Hecht and Melvin 2009); however, our results do not support that hypothesis (Chapter 1).

Annual reproductive success (nest survival and chick survival) was highly variable in North Carolina, but chick survival was the most dissimilar from survival rates on Fire Island, leading to depressed rates of reproductive output, and consequently, population decline. Differences in predator communities at each site may affect reproductive success (Cohen et al. 2009, U.S. Fish and Wildlife Service 2014, Kwon et al. 2018), and management strategies to reduce anthropogenic disturbance also differ in their extent, both between Fire Island and North Carolina, but also within the management units in North Carolina (National Park Service 2010). Chick survival in North Carolina has not appeared to change in response to anthropogenic management strategies, however, suggesting other factors (e.g., predation) may be driving this long-term trend.

The inability to reach the minimum reproductive rate needed to maintain a stationary population in North Carolina is evidence of a declining population during our

study. This rate, however, has never been met in over 30 years of monitoring and management in North Carolina, yet the population has grown in some years (Schweitzer 2017). From our evidence, it appears that North Carolina maintains its breeding plover population through immigration from other, as yet unknown, areas of the Atlantic Coast, but records of long-distance immigration are scarce (but see Hillman et al. 2012). However, if our estimates of reproductive output and survival are representative of long-term trends, immigration likely sustains the population. Further investigation into the metapopulation dynamics of North Carolina and the rest of the Southern Recovery Unit (U.S. Fish and Wildlife Service 1996) are needed to identify the specific relationships of the North Carolina population with its nearest neighbors.

While the North Carolina population may be partially sustained by immigration, efforts to increase reproductive output continue. Specifically, current management strategies designed to limit the negative effects of human disturbance on nesting plovers and broods have been in use at Cape Hatteras National Seashore (hereafter, 'CAHA') since 2008, with some alterations in protocols since. The current use of exclusion buffers around plover broods to limit this disturbance is predicated on adequate staffing resource to maintain continuous monitoring during daylight hours, but the efficiency of this monitoring may be improved if broods moved predictably.

We found daily brood movements to be variable. We expected to see larger movements as age increases, given the increased mobility and homeothermic ability of older chicks (Schekkerman and Visser 2001, Ruthrauff and McCaffery 2005), but this relationship was not significant. Environmental factors such as weather (temperature and precipitation) also did not influence daily movement rates. More surprisingly, annual variation in daily

movement rates was not well supported. We expected that the large annual differences in available habitat — primarily driven by tropical storm-related rainfall and flooding in 2016 — would be a factor in daily brood movements based on our field observations. While our results from testing this hypothesis were not significant, the regression coefficients did suggest some annual variability. Additional study examining the variation of annual habitat availability to brood movement may clarify this relationship, especially since plovers often are habitat limited (Anteau et al. 2014, Catlin et al. 2014, Fraser and Catlin 2019 in press).

The hourly rate of brood movement was variable. While many factors influence animal movements, such as predation risk and habitat quality (Laing and Raveling 1993, Kosztolányi et al. 2007, Haffner et al. 2009), we did not find that these factors explained any more variation in brood movement rates than brood age, although age also was a poor predictor. However, these factors have previously been shown to affect other types of behavior, such as foraging rates and time devoted to vigilance (Flemming et al. 1988, Loegering and Fraser 1995, Le Fer et al. 2008, Wilson and Colwell 2010, DeRose-Wilson et al. 2018). It is then possible that plover broods alter behaviors in response to these factors, instead of, or in concert with, altering movement rates, and not movement rates alone.

The movement rates that we observed during the prefledge period (51.5% were >100m/hr) suggest that if left unmonitored, broods may easily reach the boundaries of exclusion zones meant to protect them from direct and indirect risks posed by beach recreation. Crushing of chicks by vehicles is a danger, as chicks are small and cryptically colored, and therefore easily overlooked by motorists (Melvin et al. 1994). Chicks also may become stuck in deep tire ruts in highly trafficked areas (Melvin et al. 1991), and they do not appear to recognize vehicles as threats (Flemming et al. 1988), and thus might not flee from

oncoming vehicles. Possibly an exceptional example of this is when a single-chick brood crossed North Carolina Highway 12 just one day after hatching, apparently remaining within 50–150m of the highway until it reached fledging age. We did not directly observe the crossing, and therefore did not evaluate the details of its behavior, crossing duration, or timing. Based on the timing of observations, we assumed it occurred at night (B. Van Druten, USFWS, personal communication), possibly coinciding with less traffic. Leaving protective buffers also could expose chicks to trampling by pedestrians or depredation by dogs, although chicks appear to react to and avoid these stressors (Flemming et al. 1988, Burger and Niles 2012, DeRose-Wilson et al. 2018). The potential for chicks to easily reach the boundaries of the protective buffers within an hour underscores the importance of continuous monitoring by management personnel, if the current buffer sizes continued to be used. This approach, however, may be further complicated if the number of broods requiring monitoring in an area increases and surpasses available monitoring effort. Alternatively, increases in buffer sizes may lessen the need for continuous monitoring while also reducing the chance that broods move and become exposed to trampling.

At CAHA, Cape Point annually hosted the largest number of breeding plover pairs and broods, yet it is one of the most densely trafficked areas in the park for ORVs (National Park Service 2017). Due to the narrow beach at the Cape Point access and preferred foraging habitats for plovers nearby, NPS personnel often must close some or all access to Cape Point to maintain prescribed buffer sizes. Often the beach is closed due to breeding activity other than plovers (e.g., colonial waterbird nesting), potentially providing larger exclusion buffer sizes for plover broods than they might receive in the absence of other species (Chapter 2, Fig. 2). Therefore, we were unable to address the direct effect of the

buffer sizes on chick behavior, movement, and survival. Nonetheless, continued use of this management technique would benefit plover chicks. More study on the necessary size of buffer sizes is warranted, particularly in situations where protections for other species are not present.

The primary cause of chick loss appeared to be predation, and we did observe several deaths of plover chicks that were unrelated to human recreation. We twice observed chick depredation by ghost crab (*Ocyrodinae quadrata*), and also saw several disturbance events caused by ghost crabs to chicks and attending parents (Chapter 2). Ghost crabs presence can significantly lower nest survival (Kwon et al. 2018), although their effect on chick survival was previously thought to be indirect (Wolcott and Wolcott 1999; but see Loegering et al. 1995). We and NPS personnel also observed potential depredation by crows (*Corvus spp.*) on two occasions, where adult plovers were distressed, multiple crows were flying and interacting with the adult plovers, and the chicks were missing during and after the event (B. Muiznieks, NPS, personal communication). Predation is particularly difficult to quantify without directly observing the event, as there often is no conclusive evidence left (Andes et al. 2019). Ghost crabs pull chicks into burrows, and crows may immediately eat, cache, or fly away with plover chicks. However, given the apparent need for continuous monitoring of broods under current management practices (Chapter 2), additional information on the sources of chick mortality will likely be obtained. Targeted, experimental predator control, may be an important next step in management strategies to improve chick survival and reproductive output (Hunt et al. 2018).

In addition to depredation events, we also observed several instances of intraspecific aggression during brood rearing. In 2015, a non-parental plover was observed by NPS

personnel attacking a chick. The chick was individually banded, but was not identified during the event, so it was unknown if that particular chick was lost the following day. In 2017, we observed that aggression by a territorial bachelor male caused at least one chick to be injured, abandoned, and subsequently depredated by a ghost crab. The bachelor male also was observed attacking at least two other chicks in the brood, both of which appeared to be injured and were not observed again. Both of these events occurred near foraging habitat at Cape Point that is used by plover broods every year (CEW, unpublished data), including relatively dry years. In 2016, this same area of foraging habitat was available, but there also was other significant foraging resources available for several weeks due to flooding caused by heavy rainfall (Pasch and Penny 2017, Brennan 2018), and broods used these flooded areas frequently. These observations suggest a tradeoff between accessing quality foraging habitat and potential risks associated with competition with other plover pairs or broods.

We did not find evidence, however, that brood movement was driven by avoidance of conspecifics in this study. The lack of additional movement may be because plover densities are highest in and near foraging habitats, yet the cost of leaving foraging habitats is greater than the potential for injury or death caused by other plovers. However, brood movement also may expose chicks to additional non-parental plovers as the brood moves through territories (Kosztolányi et al. 2007), thus reducing a brood's tendency to move. Plovers are known to be territorial and aggressive towards competing broods (Elliott-Smith and Haig 2004), and this can increase as food availability decreases (Catlin et al. 2014). Limitation of adequate foraging resources without the risk of territorial conflict, therefore, may be a particular concern for CAHA broods. We rarely observed broods using the ocean

intertidal zone, instead they appeared to prefer low-energy moist and saturated habitats, like ephemeral pool shores, pond drainages and shorelines, and sound-side shorelines. These types of habitats typically provide greater invertebrate density and abundance than the ocean intertidal zone, and were previously linked to higher chick survival (Flemming et al. 1988, Loegering and Fraser 1995, Goldin and Regosin 1998, DeRose-Wilson et al. 2018). CAHA plovers may benefit from actions that would increase the amount or accessibility of these moist habitats, not only to provide needed sustenance, but also to potentially reduce the amount of intraspecific conflict that may depress reproductive output.

Current management at CAHA to reduce human disturbance to plover chicks was effective during our study, but additional and adaptive management strategies are needed to improve chick survival. An increase of low-energy moist foraging habitat would provide needed food resources and potentially reduce the risks associated with competition in some areas. Management to reduce common predators of chicks near nest sites and foraging areas also may improve reproductive output, as predation appeared to be an important contributor to chick mortality. Adapting current management protocols to incorporate predation and habitat influences on chick survival, in addition to continuing to reduce anthropogenic disturbance, would be a comprehensive approach to plover chick conservation.

While the breeding population at CAHA and our study sites are in decline, it appears the North Carolina barrier islands may play an outsized role for migratory plovers on the Atlantic Coast. Anecdotal reports of relatively large groups of migratory plovers in North Carolina exist (McConnaughey et al. 1990, Elliott-Smith and Haig 2004), yet the ecology of migratory plovers is poorly understood. Our work suggests the potential importance of the

North Carolina Outer Banks to Atlantic Coast Piping Plovers, given that South Point alone hosted approximately 15% of the Atlantic Coast population in 2016. With high fidelity rates during the breeding season (Catlin et al. 2015; Chapter 1) and the winter season (Gratto-Trevor et al. 2012), it seems likely that plovers maintain high fidelity rates to migratory stopover locations (Smith and Houghton 1984). This suggests that South Point, Ocracoke, and potentially other areas of the Outer Banks (McConnaughey et al. 1990, Elliott-Smith and Haig 2004), annually host large proportions of the Atlantic Coast population. No other place on the Atlantic Coast is known to host similar numbers of migrating plovers, and sites in the wintering grounds with comparable numbers are exceedingly rare (Elliott-Smith et al. 2015, D. Catlin, personal communication).

The time that plovers spent on South Point varied considerably, averaging 4–7 weeks. Although it is unknown why plovers remained for these variable amounts of time, previous work has suggested that individual condition (Lyons and Haig 1995, Weithman et al. 2017), remaining migratory distance (Lislevand et al. 2016), overall migratory strategy (Piersma 1987), stopover site quality (Tarr et al. 2010, Pandiyan and Asokan 2016), and weather conditions (Ma et al. 2011) may affect migration timing or stopover duration. Conditions during migration at these stopover locations may have widespread effects on the Atlantic Coast population (Weber et al. 1999), and further investigation into migratory behaviors such as stopover duration and timing and their relationship to other periods of the life cycle (Weithman et al. 2017) may begin to detangle these effects.

North Carolina appears to be an important place for Piping Plovers. While its breeding population is small, potential demographic interaction with the rest of the Southern Recovery Unit suggests larger consequences of reproductive output and survival of

North Carolina plovers. Continued improvement to management strategies, such as additional measures to increase chick survival, would not only benefit North Carolina plovers, but also may contribute to the growth of the Southern Recovery Unit population. This area's apparent importance to migrating Atlantic Coast plovers also may be unique and may have far reaching consequences to the species. While little work has focused directly on North Carolina plovers in the past, circumstances that exist elsewhere in the plover range (e.g., predation, habitat limitation) likely affect this population in similar ways. Combining previous findings regarding plover ecology, these new data, and further study of North Carolina plovers would be a useful, comprehensive step towards plover conservation in North Carolina and throughout the flyway.

Literature Cited

- Andes, A. K., T. L. Shaffer, M. H. Sherfy, C. M. Hofer, C. M. Dovichin, and S. N. Ellis-Felege (2019). Accuracy of nest fate classification and predator identification from evidence at nests of Least Terns and Piping Plovers. *Ibis* 161:286–300.
- Anteau, M. J., M. T. Wiltermuth, M. H. Sherfy, T. L. Shaffer, and A. T. Pearse (2014). The role of landscape features and density dependence in growth and fledging rates of Piping Plovers in North Dakota, USA. *The Condor* 116:195–204.
- Brennan, M. J. (2018). Tropical Cyclone Report: Tropical Storm Bonnie (AL022016). National Oceanic and Atmospheric Administration, National Hurricane Center, Miami, FL. 36 pages.
- Burger, J. (1994). The Effect of Human Disturbance on Foraging Behavior and Habitat Use in Piping Plover (*Charadrius melodus*). *Estuaries* 17:695–701.
- Burger, J., and L. Niles (2012). Shorebirds and stakeholders: Effects of beach closure and human activities on shorebirds at a New Jersey coastal beach. *Urban Ecosystems* 16:657–673.
- Catlin, D. H., J. D. Fraser, and J. H. Felio (2015). Demographic Responses of Piping Plovers to Habitat Creation on the Missouri River. *Wildlife Monographs* 192:1–42.
- Catlin, D. H., O. Milenkaya, K. L. Hunt, M. J. Friedrich, and J. D. Fraser (2014). Can river management improve the Piping Plover's long-term survival on the Missouri River? *Biological Conservation* 180:196–205.

- Cohen, J. B., J. D. Fraser, and D. H. Catlin (2006). Survival and site fidelity of Piping Plovers on Long Island, New York. *Journal of Field Ornithology* 77:409–417.
- Cohen, J. B., L. M. Houghton, and J. D. Fraser (2009). Nesting Density and Reproductive Success of Piping Plovers in Response to Storm- and Human-Created Habitat Changes. *Wildlife Monographs* 173:1–24.
- DeRose-Wilson, A. L., K. L. Hunt, J. D. Monk, D. H. Catlin, S. M. Karpanty, and J. D. Fraser (2018). Piping Plover Chick Survival Negatively Correlated With Beach Recreation. *The Journal of Wildlife Management* 82:1608–1616.
- Elliott-Smith, E., and S. M. Haig (2004). Piping Plover (*Charadrius melodus*). In *The Birds of North America online* (A. F. Poole, Editor). Cornell Lab of Ornithology, Ithaca, NY, USA. <https://birdsna.org/Species-Account/bna/species/pipplo/> Accessed 15 January 2019.
- Elliott-Smith, E., M. Bidwell, A. E. Holland and S. M. Haig (2015). Data from the 2011 International Piping Plover Census: U.S. Geological Survey Data Series 922. Department of the Interior, U.S. Geological Survey. Reston, VA. 296 pages.
- Flemming, S. P., R. D. Chiasson, P. C. Smith, P. J. Austin-Smith, and R. P. Bancroft (1988). Piping Plover Status in Nova Scotia Related to Its Reproductive and Behavioral Responses to Human Disturbance. *Journal of Field Ornithology* 59:321–330.
- Fraser, J. D. and D. H. Catlin (2019). Habitat ecology and conservation of *Charadrius* plovers. In *Population Ecology and Conservation of Charadrius plovers*. Studies in Avian Biology (Colwell, M.A. and S.M. Haig, eds.), CRC Press. *In press*.

- Goldin, M. R., and J. V. Regosin (1998). Chick Behavior, Habitat Use, and Reproductive Success of Piping Plovers at Goosewing Beach, Rhode Island. *Journal of Field Ornithology* 69:228–234.
- Gratto-Trevor, C., D. Amirault-Langlais, D. Catlin, F. Cuthbert, J. Fraser, S. Maddock, E. Roche, and F. Shaffer (2012). Connectivity in Piping Plovers: Do Breeding Populations Have Distinct Winter Distributions? *Journal of Wildlife Management* 76:348–355.
- Haffner, C. D., F. J. Cuthbert, and T. W. Arnold (2009). Space use by Great Lakes Piping Plovers during the breeding season. *Journal of Field Ornithology* 80:270–279.
- Hecht, A., and S. M. Melvin (2009). Population Trends of Atlantic Coast Piping Plovers, 1986–2006. *Waterbirds* 32:64–72.
- Hillman, M. D., S. M. Karpanty, J. D. Fraser, F. J. Cuthbert, J. M. Altman, T. E. Borneman, and A. Derosé-Wilson (2012). Evidence for Long-distance Dispersal and Successful Interpopulation Breeding of the Endangered Piping Plover. *Waterbirds* 35:642–644.
- Hunt, K. L., S. M. Karpanty, K. L. Davis, A. Wilke, N. Myers, C. Spiegel, S. Shulte, D. H. Catlin, J.D. Fraser (2018). Guidance and Best Practices for Coordinated Predation Management to Benefit Temperate Breeding Shorebirds in the Atlantic Flyway. 261 pages.
- Kosztolányi, A., T. Székely, and I. C. Cuthill (2007). The function of habitat change during brood-rearing in the precocial Kentish plover *Charadrius alexandrinus*. *Acta Ethologica* 10: 73–79.

- Kwon, E., J. D. Fraser, D. H. Catlin, S. M. Karpanty, C. E. Weithman, and B. Muiznieks (2018). Presence of Ghost Crabs and Piping Plover Nesting Success. *Journal of Wildlife Management* 82:850–856.
- Laing, K. K., and D. G. Raveling (1993). Habitat and Food Selection by Emperor Goose Goslings. *Condor* 95:879–888.
- LeDee, O. E., T. W. Arnold, E. A. Roche, and F. J. Cuthbert (2010). Use of Breeding and Nonbreeding Encounters to Estimate Survival and Breeding-Site Fidelity of the Piping Plover at the Great Lakes. *Condor* 112:637–643.
- Le Fer, D., J. D. Fraser, and C. D. Kruse (2008). Piping Plover Foraging-Site Selection on the Missouri River. *Waterbirds* 31:587–592.
- Lislevand, T., M. Briedis, O. Heggøy, and S. Hahn (2016). Seasonal migration strategies of Common Ringed Plovers *Charadrius hiaticula*. *Ibis* 159:225–229.
- Loefering, J. P., and J. D. Fraser (1995). Factors Affecting Piping Plover Chick Survival in Different Brood-rearing Habitats. *Journal of Wildlife Management* 59:646–655.
- Loefering, J. P., J. D. Fraser, and L. L. Loefering (1995). Ghost Crab Preys on a Piping Plover Chick. *The Wilson Bulletin* 107: 768–769.
- Lyons, J. E., and S. M. Haig (1995). Fat Content and Stopover Ecology of Spring Migrant Semipalmated Sandpipers in South Carolina. *Condor* 97:427–437.
- Ma, Z., N. Hua, X. Zhang, H. Guo, B. Zhao, Q. Ma, W. Xue, and C. Tang (2011). Wind conditions affect stopover decisions and fuel stores of shorebirds migrating through the

south Yellow Sea. *Ibis* 153:755–767.

McConnaughey, J. L., J. D. Fraser, S. D. Coutu, and J. P. Loegering (1990). Piping Plover Distribution and Reproductive Success on Cape Lookout National Seashore.

Unpublished report to the National Park Service. 89 pages.

Melvin, S. M., C. R. Griffin, and L. H. Macivor (1991). Recovery strategies for Piping Plovers in managed coastal landscapes. *Coastal Management* 19:21–34.

Melvin, S. M., A. Hecht, and C. R. Griffin (1994). Piping Plover Mortalities Caused by Off-Road Vehicles on Atlantic Coast Beaches. *Wildlife Society Bulletin* 22:409–414.

National Park Service (2010). Cape Hatteras National Seashore Off-Road Vehicle Management Plan: Final Environmental Impact Statement. National Park Service, Cape Hatteras National Seashore, Manteo, NC. 274 pages.

National Park Service (2017). Cape Hatteras National Seashore Annual Park Recreation Visitation Report. Available at <https://irma.nps.gov/Stats/SSRSReports>. Accessed 25 January 2019.

Pandiyan, J., and S. Asokan (2016). Habitat use pattern of tidal mud and sand flats by shorebirds (charadriiformes) wintering in southern India. *Journal of Coastal Conservation* 20:1–11.

Pasch, R. J., and A. B. Penny (2017). Tropical Cyclone Report; Tropical Storm Colin (AL032016). National Oceanic and Atmospheric Administration, National Hurricane Center, Miami, FL, 29 pages.

Piersma, T. (1987). Hop, Skip or jump? Constraints on migration of arctic waders by

- feeding, fattening and flight-speed. *Limosa* 60:185–194.
- Ruthrauff, D. R., and B. J. McCaffery (2005). Survival of Western Sandpiper broods on the Yukon-Kuskokwim Delta, Alaska. *Condor* 107:597–604.
- Schekkerman, H., and G. H. Visser (2001). Prefledging energy requirements in shorebirds: energetic implications of self-feeding precocial development. *The Auk* 118:944–957.
- Schweitzer, S. H. (2017). 2017 Breeding Season Report for the Piping Plover in North Carolina. Unpublished report. North Carolina Wildlife Resource Commission. New Bern, NC. 6 pages.
- Smith, P. W., and N. T. Houghton (1984). Fidelity of Semipalmated Plovers to a Migration Stopover Area. *Journal of Field Ornithology* 55:247–249.
- Tarr, N. M., T. R. Simons, and K. H. Pollock (2010). An Experimental Assessment of Vehicle Disturbance Effects on Migratory Shorebirds. *Journal of Wildlife Management* 74:1776–1783.
- U.S. Fish and Wildlife Service (1996). Piping Plover (*Charadrius melodus*), Atlantic Coast Population, Revised Recovery Plan. U.S. Fish and Wildlife Service. Hadley, MA.
- U.S. Fish and Wildlife Service (2014). Biological Opinion and Conference Opinion, Fire Island Inlet to Moriches Inlet, Fire Island Stabilization Project. U.S. Fish and Wildlife Service. Suffolk County, NY.
- Weber, T. P., A. I. Houston, and B. J. Ens (1999). Consequences of Habitat Loss at Migratory Stopover Sites : A Theoretical Investigation. *Journal of Avian Biology* 30:416–426.

- Weithman, C., D. Gibson, K. Hunt, M. Friedrich, J. Fraser, S. Karpanty, and D. Catlin (2017). Senescence and carryover effects of reproductive performance influence migration, condition, and breeding propensity in a small shorebird. *Ecology and Evolution* 7:11044–11056.
- Wilson, C. A., and M. A. Colwell (2010). Movements and Fledging Success of Snowy Plover (*Charadrius alexandrinus*) Chicks. *Waterbirds* 33:331–340.
- Wolcott, D. L., and T. G. Wolcott (1999). High Mortality of Piping Plovers on Beaches with Abundant Ghost Crabs: Correlation, Not Causation. *The Wilson Bulletin* 111:321–329.

APPENDIX B

3/4/2019

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Figure 1. Letter of copyright release for Chapter 3, “Discovery of an Important Stopover Location for Migratory Piping Plovers (*Charadrius melodus*) on South Point, Ocracoke Island, North Carolina, USA” from Andrew Kasner, editor of *Waterbirds*.