

**POPULATION DYNAMICS OF PIPING PLOVERS
ON THE NIOBRARA RIVER, NEBRASKA**

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POPULATION DYNAMICS AND HABITAT SELECTION OF PIPING PLOVERS ON THE NIOBRARA RIVER, NEBRASKA

Meryl J. Friedrich

Abstract

Prairie rivers of the Great Plains, USA, provide important habitat for the federally threatened piping plover (“plover”, *Charadrius melodus*). Plovers nest on open to sparsely vegetated river sandbars, and their demographic rates are closely linked to habitat availability and quality, as well as river flow. The Niobrara River in northern Nebraska has supported 22–41% of the state’s plovers since species listing in 1986, but the population and habitat are relatively understudied, and both have declined since 2010. The objectives of this study were to understand plover demography, habitat, and the role of the Niobrara in the regional plover population.

Periods of high river flow promote creation and maintenance of suitable sandbar nesting habitat, but increased river flow during the plover breeding season can decrease nest and chick survival. We estimated the effect of daily peak river flow on survival rates of 115 nests and 66 chicks on the Niobrara River, 2010–2016, using logistic exposure and Cormack-Jolly-Seber models, respectively. We monitored 1,874 banded hatch-year and adult birds across the regional population (Niobrara River, Lewis and Clark Lake, Gavins Point Reach segment of the Missouri River), and used multi-state mark-recapture models to estimate survival and inter-annual dispersal probabilities among sites relative to habitat availability. We developed land cover datasets from high-resolution aerial imagery to quantify suitable habitat and compare the relative effects of habitat characteristics on nest-site selection and nest success for a subset of years (2010, 2012, 2014, and 2016) using logistic regression models. We included data from a sympatric nester with similar nesting habitat needs, the interior least tern (“tern”, *Sterna antillarum athalassos*), to improve precision of our models. We compared 63 plover and 92 tern nests to 292 random unused points, and 73 successful (hatched ≥ 1 egg) to 79 failed nests.

Low nest and chick survival and high emigration from the Niobrara appear to be important factors contributing to population decline. Daily nest and chick survival were negatively related to river flow. Nest-site selection was based primarily on distance to the river bank (i.e., the nearest potential source of predators), yet flooding (eggs submerged or washed out of the nest bowl during increased river flow) caused at least as many nest failures as predation. Nests predominantly were surrounded by dry sand habitat, indicating some degree of flood avoidance, but were no farther from water than random, and drier nest sites were no less likely to fail. Dispersal occurred

throughout the regional population, but plovers were more likely to leave the Niobrara than to enter it. Expansive flood-created sandbars on the Missouri River, concurrent with a trend towards more vegetated and saturated habitat on the Niobrara, may have drawn birds from the Niobrara population, especially those that dispersed to the Niobrara during sustained Missouri River flooding 2010–2011.

The outsized negative effect of flooding on nest success, the lack of protection afforded by dry sand nest sites, and selection for nesting habitat based more strongly on predator avoidance than flood avoidance suggest that plovers may have face more frequent and intense levels of breeding season flooding than is typical. Identifying and promoting the processes that contribute to creation and maintenance of high-elevation sandbars on the Niobrara is an important next step towards effective management of nesting birds.

General Audience Abstract

Prairie rivers of the Great Plains, USA, provide important habitat for a federally threatened shorebird, the piping plover (“plover”, *Charadrius melodus*). During their breeding season (April–August), plovers nest and raise chicks on open to sparsely vegetated areas of river sandbars, and their survival and reproductive success are closely tied to amount and quality of sandbar habitat. The number of plovers on the Niobrara River in northeast Nebraska has declined since 2010, and in this study our objectives were to monitor nests, chicks, and adult birds to document plover survival, movement among neighboring sites, reproductive success, and habitat changes on the Niobrara from 2010–2016.

Because plovers nest on the sand, they can lose nests and chicks when river flow increases and washes over sandbars (“flooding”). We found that nest and chick survival sharply decreased when river flow was high. Plovers chose nest sites in dry sand areas, which are typically the tallest part of a sandbar and most protected from flooding, but these nests were no more likely to hatch than those in areas with wetter (lower elevation) sand. Plovers primarily chose nest sites far from the river bank, which was the nearest potential source of predators, yet flooding caused at least as many nest failures as predation. Plovers moved between the Niobrara and nearby Missouri River, but overall were much more likely to leave the Niobrara than to enter it. Expansive sandbar creation on the Missouri River, concurrent with a trend towards lower-quality (more vegetated and saturated) habitat on the Niobrara, may have drawn birds from the Niobrara population, especially those displaced from the Missouri during sustained flooding 2010–2011.

Movement to the Missouri River and low nest and chick survival due to flooding contributed to population decline on the Niobrara. The outsized effect of flooding on nest success, the lack of protection afforded by dry sand nest sites, and selection for nesting habitat based more strongly on predator avoidance than flood avoidance suggests that plovers face more frequent and intense levels of breeding season flooding than is typical. Identifying and promoting the processes that contribute to creation and maintenance of high-elevation sandbars on the Niobrara is an important next step towards effective management of nesting birds.

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INTRODUCTION

The piping plover (“plover”; *Charadrius melodus*) is a North American shorebird that breeds in open sand and gravel habitats along the Atlantic coast, shorelines of the Great Lakes, and on prairie rivers, wetlands, and alkaline lakes of the Great Plains (Elliott-Smith and Haig 2004). The species was granted protection under the Endangered Species Act in 1986 following range-wide population declines (USFWS 1985). In the Great Plains, river systems support nearly half of the plover population in some years, and the destruction and modification of habitat attributed to river channelization and modified river flow poses a high level of threat to the plover population (USFWS 2015).

The Niobrara River in northern Nebraska hosts a rich diversity of plants and wildlife (Johnsgard 2007) and has supported 22–41% of Nebraska’s plover population since the species was listed (Sidle et al. 1991, Plissner and Haig 2000, Ferland and Haig 2002, Elliott-Smith et al. 2009, 2015), with records of nesting plovers dating to 1903 (Bruner et al. 1903). Although there are several engineered structures and streamflow diversions (Alexander et al. 2009), the Niobrara is one of the last minimally regulated rivers in the Great Plains (Ethridge et al. 1999) that supports breeding plovers (Sidle et al. 1991, Plissner and Haig 2000, Ferland and Haig 2002, Elliott-Smith et al. 2009, 2015). Monitoring, research, and management of populations nesting on heavily modified rivers (e.g., the Missouri River; Catlin et al. 2015) have demonstrated an important role of habitat and river flow in regulating plover and tern populations (Catlin et al. 2011, Anteau et al. 2014, USFWS 2015). Anthropogenic alteration of river flow for flood control, irrigation, hydropower, and other purposes, can inundate nests and reduce the quantity and quality of sandbar habitat by inhibiting sediment deposition, allowing for vegetation encroachment (Benjankar et al. 2012) and establishment (Currier 1982), and intensifying sandbar erosion (Schmidt and Graf 1990, Hazel et al. 2010). Threats to reproductive success, such as predation and prey availability, are also related to the amount of habitat, directly or indirectly (USFWS 2015, Hunt et al. 2018). Because of the relatively “natural” state of the Niobrara River, it has been proposed as a model system for guiding water management strategies on modified rivers (e.g., the Missouri River) that are actively managed for piping plovers (Adolf et al. 2001).

Despite the Niobrara River’s relatively uninterrupted flow, and stability or growth in the regional piping plover population (Andres et al. 2012, Hunt et al. 2018), the Niobrara River plover population has declined since 2010, prompting inquiry to the underlying drivers. One previous study of Niobrara River plover demography indicated that the river supported a relatively large breeding population, with nest and fledging success rates similar or greater than other populations, and suggested that there was interchange within the regional population when habitat suitability fluctuated among sites (Adolf et al. 2001). The overall objectives of this

study are to document piping plover demography and habitat availability on the Niobrara River and determine how this population relates to the larger Great Plains population. In Chapter I, I estimated survival of nests, chicks, hatch-year birds, and adult birds, as well as regional movements of breeding birds, and I related these demographic parameters to changes in river flow and habitat availability. In Chapter II, I compared habitat features between nest sites and randomly selected unused points and explored the relationship between nest habitat characteristics and reproductive success. The second chapter also incorporates nest selection and success data from a sympatric nester, the endangered interior least tern (*Sterna antillarum athalassos*).

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CHAPTER I: DEMOGRAPHY OF PIPING PLOVERS ON THE NIOBRARA RIVER, NEBRASKA

Abstract

Dams alter the natural hydrology of rivers, and their adverse impacts on downstream riparian areas are well established. However, impacts on upstream tributaries are poorly understood. Mainstem dams on the Missouri River regulated water flow and reduced sediment transport, causing morphological and hydrological changes on a major inter-dam tributary, the Niobrara River. Since 2010, the population of a sandbar-nesting shorebird, the piping plover (“plover”, *Charadrius melodus*) using the Niobrara River has declined. We investigated how hydrology and habitat availability affected plover demographic rates on the Niobrara River and nearby breeding sites on the Missouri River 2010–2016. Nest survival rates from logistic exposure models were negatively related to water flow rates on both the Niobrara River and a flow-through reservoir on the Missouri River, Lewis and Clark Lake (Niobrara = 0.21, 95% CI: 0.11–0.38, Lewis and Clark Lake = 0.23, 95% CI: 0.14–0.36), but nests failed due to flooding on the Niobrara (43%) more frequently than on Lewis and Clark Lake (5%), and the effect of flow on nest survival was 1.7 times greater on the Niobrara than on Lewis and Clark Lake. Likewise, chick survival, estimated from a Cormack-Jolly-Seber model, decreased with water flow on the Niobrara ($\beta_{\text{NIO:flow}} = -1.21$, 95% CI = -1.63– -0.79) and had a higher rate of decline after flows exceeded 1 SD above the mean. Breeding dispersal among sites was highest from the Niobrara to Lewis and Clark Lake (0.51 ± 0.07 ; mean \pm SE) and overall, both adult and hatch-year plovers were more likely to leave the Niobrara population than to enter it. Relatively high nest loss to flooding, declines in the amount of habitat through sediment aggradation, and differences in habitat quality among the sites likely contributed to emigration from the Niobrara River. As habitat on Lewis and Clark ages and becomes less suitable (e.g., through vegetation encroachment and bank erosion), ensuring alternate sources of habitat, like the Niobrara, is important for sustaining the regional population. Understanding ecological effects of reservoir sedimentation on upstream tributaries is integral to management decisions regarding conservation value of sedimentary deltas.

Introduction

Widespread dam construction has changed water flow and sediment transport regimes (Poff et al. 1997, Graf 1999), ecosystem structures and processes (Poff and Zimmerman 2010), and consequently has altered riparian areas worldwide (World Commission on Dams 2000). Studies of environmental impacts of dams largely have focused on downstream effects of altered hydrology and sediment supplies (Ligon et al. 1995, Nilsson and Berggren 2000); however, ecological changes also occur upstream of impoundments (Pringle 1997). In particular, sedimentary deltas form in regulated river systems where mainstem river and tributary streams flow into reservoirs (Petts 1979). This long-term impact of dams (Rosenberg et al. 1997) has emerged as aging 20th century reservoirs slowly accumulate sediment (Palmieri et al. 2001). The conservation value of these novel ecosystems is debated because they contain species and communities similar to pre-dam conditions (Johnson 2002) and could contribute to ecological restoration of regulated rivers (Volke et al. 2015), but also deprive lower reaches of sediment (National Research Council of the National Academics 2011) and raise water and sediment levels in upstream tributaries (Bristow et al. 1999). To date, discussion on the potential ecological effects of sedimentation have focused primarily on the regulated river, with effects on upstream tributaries being poorly studied.

The Niobrara River is a major tributary to the Missouri River and contributes approximately 40% of the annual sediment load to the Lewis and Clark Lake reservoir into which it flows (Coker et al. 2009). Mainstem dams on the Missouri River above and below the Niobrara-Missouri confluence modulate the Missouri River's flow and reduce the Missouri River's ability to clear sediment from the mouth of the Niobrara, resulting in formation of a sedimentary delta (Ethridge et al. 1999, Bristow et al. 1999). Near the river mouth, the Niobrara has transitioned from a relatively deep, stable channel with large sandbars to become increasingly braided and shallow (Skelly et al. 2003), and it has filled with sediment to the extent that the channel bed is elevated above the adjacent floodplain (Resource Consultants and Engineers, Inc. 1993, Ethridge et al. 1999). The potential impacts of these hydrological and morphological changes on Niobrara riverine habitat and species are largely unknown, but generally, flow alteration often has an overwhelmingly negative effect on ecosystem metrics (Poff and Zimmerman 2010).

The Niobrara River supports a rich diversity of plants and animals (Johnsgard 2007), including a rare sandbar-nesting shorebird, the piping plover ("plover", *Charadrius melodus*). The Great Plains breeding population of plovers was designated federally threatened in 1986, partially due an altered hydrograph (USFWS 2003) and subsequent loss of riverine sandbar breeding and brood-rearing habitat on the Missouri and other rivers (USFWS 2009). Creation and maintenance of early successional sandbar habitat requires peak flows high enough and long enough to deposit sediment and scour existing vegetation (Benjankar et al. 2012), followed

by steady low flows to minimize erosion (Schmidt and Graf 1990, Hazel et al. 2010, Alvarez and Schmeekle 2013). Interruption of the natural hydrograph and sediment transport capability of a river can contribute to steep reductions in the amount of sandbar habitat (Dixon et al. 2012) and affect the suitability of sandbar habitat for species. The Niobrara River has supported 22–41% of Nebraska’s plover population since the species was listed (Sidle et al. 1991, Plissner and Haig 2000, Ferland and Haig 2002, Elliott-Smith et al. 2009, 2015). However, since 2010, the Niobrara plover population has declined despite stability or growth in the regional population (Andres et al. 2012, Hunt et al. 2018).

The plover population decline on the Niobrara River followed unprecedented flooding on the Missouri River that resulted in expansive sandbar habitat creation and subsequent growth in the Missouri River plover population (Hunt et al. 2018). Plovers are disturbance adapted, quickly colonize newly created or exposed sand habitats (Gaines and Ryan 1988, Cohen et al. 2009, Catlin et al. 2015), and are capable of considerable dispersal between years (Haig and Oring 1988a). Shifting habitat availability on the Niobrara and Missouri rivers may have motivated movements between the two populations and therefore may be an important factor explaining the observed population decline on the Niobrara River.

Increased water flow can negatively affect plover reproductive success by submerging nests and washing away chicks (Grover and Knopf 1982, Faanes 1983, Sidle et al. 1992). Sandbars that are low in elevation relative to water level are particularly susceptible to inundation. As the Niobrara River becomes increasingly braided and shallow (Skelly et al. 2003), the potential for fluctuating water flow to inundate sandbars may increase. This trend may be further intensified by climate-related factors. There is a long-term upward trend in streamflow in the Niobrara watershed (Norton et al. 2014) and an increase in the frequency and intensity of extreme precipitation events in the central U.S. (Kunkel et al. 2012). Intensification of storms may increase frequency and magnitude of flash flooding (Feng et al. 2016). Although flooding is a natural disturbance event on unmodified rivers, anthropogenic and climate-related hydrological changes present challenging and novel conditions to species, such as plovers, that are adapted to the specific disturbance regime of the landscape (Lytle and Poff 2004).

We investigated factors contributing to the observed decline in plovers on the Niobrara River 2010–2016 in the first demographic analysis of this population since 1997 (Adolf et al. 2001). Our objective was to estimate demographic parameters and explore the influence of water flow and habitat availability on the population decline. We derived nest and chick survival rates on the Niobrara and an adjacent site on the Missouri River, Lewis and Clark Lake, to compare rates between sites. We also examined survival and regional movements of breeding adults among the Niobrara, Lewis and Clark Lake, and a third nearby site on the Missouri River, the Gavins Point Reach. We expected that increased river flow would reduce nest and chick survival, and that adults would disperse from the Niobrara in years when habitat

was relatively more abundant at other breeding sites. Identification of demographic mechanisms contributing to population decline and the factors affecting those mechanisms can help determine what, if any, management actions may be effective in improving the Niobrara River plover population and contribute to understanding the ecological effects of reservoir sedimentation.

Methods

Study Species

The piping plover is a rare North American shorebird that breeds in three regions: the Atlantic Coast, the Great Lakes, and the Great Plains. On riverine habitats in the Great Plains, plovers select open to sparsely vegetated emergent sandbars for nesting and brood-rearing. The nest bowl is a small, shallow scrape (8–9 cm wide, 1–2 cm deep) that may be lined with a thin layer of pebbles. A typical nest has four eggs, laid over the course of approximately six days (Wilcox 1959, Whyte 1985, Haig and Oring 1988a), and is incubated in intervals by both adults. Chicks hatch after approximately 28 days of incubation and leave the nest soon after. Chicks forage for invertebrate prey, preferentially on moist substrates (Le Fer et al. 2008), and fledge at approximately 25 days post-hatch. Renesting following nest failure may occur multiple times in a breeding season, but producing multiple successful nests in a year is rare (Hunt et al. 2015).

Study Area

We studied plovers at three breeding sites in the Great Plains, USA 2010–2016 (Figure 1): the Niobrara River (NIO), the Lewis and Clark Lake segment of the Missouri River (LCL), and the Gavins Point Reach segment of the Missouri River (GVP). We studied nest and chick survival on NIO and LCL, and estimated survival and regional movements of adults among NIO, LCL, and GVP.

The Niobrara River is a sixth order stream that runs approximately 860 km, from headwaters in southeastern Wyoming across northern Nebraska to its confluence with the Missouri River. The Niobrara study site comprised approximately 130 river km between the Nebraska State Highway 137 bridge north of Newport, NE (42°47'N, 99°20'W) and the river mouth at Niobrara, NE (42°45'N, 98°03'W). It was divided at approximately river km 65 by Spencer Dam, a hydroelectric facility through which water runs freely. In our study area, the river is characterized by a wide valley and channel and a persistently braided pattern, with clusters of emergent sandbars (Alexander et al. 2010). Flow is driven by groundwater, with the effects of flashier, precipitation-runoff hydrology becoming more prominent in the easternmost third of the river (Alexander et al. 2009). Adjacent land cover is a mix of marsh floodplain, wooded riparian corridor, wetlands, natural floodplain and upland forest communities, pastureland, and croplands, and the 32 km stretch upstream from the mouth is part of the Missouri National Recreational River.

The Missouri River is a ninth order stream and one of the largest rivers in North America (Kammerer 1990, Pierson 2008). Our study area included two segments of the Missouri River: the Lewis and Clark Lake site consisted of approximately 85 river km between the Fort Randall Dam near Pickstown, SD (43°04'N, 98°33'W) and the reservoir formed by the Gavins Point Dam in Yankton, SD (42°51'N, 97°29'W). The Gavins Point Reach site comprised approximately 95 river km from the Gavins Point Dam to Ponca State Park, NE (42°36'N, 96°42'W). These segments were separated by approximately 25 km of open water (Lewis and Clark Lake reservoir). The Gavins Point Reach segment and much of the Lewis and Clark segment are part of the Missouri National Recreational River. Surrounding land cover is riparian forest, wetlands, grassland, and increasingly agriculture (Dixon et al. 2012). A series of six large mainstem dams built for flood control, hydroelectric power, and transportation regulate water flow on the Missouri. In the spring and summer of 2010 and 2011, historic rainfall and flooding (Vining et al. 2013) resulted in substantial changes in the area and arrangement of sandbars on the Missouri River (Cowman 2012, Hunt et al. 2018) and built sandbars high in elevation relative to typical water level (Johnson et al. 2015).

Data Collection

Nest monitoring. We located plover nests on open sand to sparsely vegetated areas of emergent sandbars during the plover breeding season (20 April–20 August) by grid searching and using behavioral cues from adult birds. Upon location, we logged each nest point using a handheld GPS unit (Trimble Geo XT, Trimble Navigation, Ltd., Sunnyvale, CA). We floated each egg to estimate incubation (Westerskov 1950) and hatch date (34 days from nest initiation; Elliott-Smith and Haig 2004). We attempted to check each nest every 2–7 days to determine nest fate, increasing our visit frequency within 3 days of the estimated hatch date when possible. We considered a nest successful if we observed ≥ 1 chicks or if ≥ 1 egg disappeared ± 2 days from the estimated hatch date, without sign of failure (e.g., predator tracks, eggs washed out of nest bowl; Catlin et al. 2015). Although it is a common management practice to use predator exclosures on plover nests (Melvin et al. 1992), none of the nests in this study were exclosed. We monitored nests on the lower section of the Niobrara River (downstream of Spencer Dam) 2010–2016 and on Lewis and Clark Lake 2012–2016. Nests on LCL were inconsistently monitored in 2010, and flooding for the duration of the 2011 breeding season led to abnormally high nest densities and low nest success (Catlin et al. 2015), so we did not include those years in this study.

Chick monitoring. As soon after hatching as possible, we captured chicks by hand and marked them with a unique color band combination. We calculated chick age at banding based on known or estimated hatch date. We attempted to recapture or resight chicks every 2–5 days until fledging (approximately 25 days of age; Hunt et al. 2013). We monitored chicks on the lower section of the Niobrara 2011–2016 and on Lewis and Clark Lake 2010–2016.

Adult monitoring. We searched for banded plovers on each site in each year, with different frequency depending on project focus and bird activity. In each year that we monitored nests on a given site, we captured and uniquely marked incubating adult birds with a combination of plastic color leg bands. Our observations of banded birds also include individuals marked during previous demography studies at GVP and LCL since 2005 (Catlin et al. 2015, Hunt et al. 2018). We designated two levels of survey effort in detection probability models (2011–2014 and 2015–2016) to account for differences in survey frequency. We conducted at least two surveys per year on NIO. On LCL and GVP in 2011–2014, we surveyed approximately every other day, with the exception of GVP in 2011 when high water flow submerged all sandbars throughout the majority of the breeding season. In 2015–2016, we surveyed LCL approximately every 3–4 days and we surveyed GVP once and supplemented GVP survey data with camera trap videos of nesting adults (U.S. Army Corps of Engineers, unpublished data).

Water flow data. We used 15-minute hydrographic data (hereafter, “water flow”) obtained through the United States Geological Survey National Water Information System (<https://waterdata.usgs.gov/nwis>) in models predicting plover nest and chick survival on NIO and LCL. Stream gages were selected based on proximity to the breeding sites. For NIO, we used data from the stream gage near Verdel, NE (<13 river km from any monitored nest on NIO; gage # 06465500, 42°44'N, 98°13'W), measured as water discharge rate (m^3/s). For LCL, the nearest stream gage was below Ponca Creek near Verdel, NE (<29 river km from any monitored nest on LCL; gage # 06453620, 42°46'N, 98°03'W). Water discharge rate was not available at this site, so for LCL we obtained water gage height (m). We standardized (mean = 0.0, SD = 1.0) water flow data separately for NIO and LCL to account for this discrepancy in units and to allow for cross comparisons of the effect of relative water flow between the two sites. Because of our interest in the effect of flooding on survival, we condensed the 15-minute water flow data to the maximum value recorded at a gage during each nest or chick survival interval.

Habitat data. We classified land cover from remote sensed imagery to estimate the area of plover nesting habitat (dry or wet sand, $\leq 30\%$ ground cover) for models predicting movement probability. We obtained Niobrara River imagery from the National Agricultural Imagery Program (2012, 2014, and 2016; ≤ 1 m resolution) and from Landsat 8 (2013, 2015; 30 m resolution). We classified imagery using object-oriented methods in eCognition Essentials (Trimble 2016). The two-step classification process entailed 1) multiresolution segmentation, in which adjacent pixels sharing common spectral characteristics were grouped into objects based on user-defined size, shape, and texture parameters, and 2) a supervised classification of the objects. We acquired land cover data for the Missouri River (2012–2016) produced by the U.S. Geological Survey from pan-sharpened multispectral QuickBird (satellite) imagery using object-

oriented methods in Definers Developer (L. Strong, pers. comm.). Imagery was acquired each year between April and October.

Statistical Analyses

Nest survival. We used random effects logistic exposure models (Rotella et al. 2004, Shaffer 2004) to estimate daily survival rate of plover nests at NIO and LCL in relation to water flow. We predicted that survival would decrease with water flow because elevated flow could submerge sandbars and flood nests (Sidle et al. 1992, Espie et al. 1998). We included variables for nest age (in days), clutch size, and day of year (standardized to 20 April = day 0) to account for other sources of variation. We expected that nest survival would increase with nest age and clutch size and would decrease with day of year based on previous work in this system (Catlin et al. 2015). We included a random effect (sandbar \times year) to control for annual, sandbar-specific variation in all models. In addition to the random effect, we tested for a fixed effect of year by adding it to the global model prior to the full analysis. We tested fit of the global model with a Hosmer and Lemeshow goodness-of-fit test (Shaffer 2004, Hosmer et al. 2013). We performed a separate analysis for each site to isolate site-specific variation.

Chick survival. We used a Cormack-Jolly-Seber model to estimate age-specific daily survival and detection probability of chicks from hatch to fledge (25 days) at NIO and LCL in relation to water flow. We predicted that increases in water flow would negatively affect chick survival, either directly by flooding chicks (Sidle et al. 1992) or indirectly by reducing habitat availability (Espie et al. 1998). We included variables for year (2010–2016), natal site (NIO or LCL), hatch date (standardized to 20 April = 0), and age at banding (in days since hatch, linear or categorical) to account for other sources of variation in survival. We expected that earlier hatch date and older age at banding would increase estimates of chick survival based on survival patterns in other studies (Saunders et al. 2014, Catlin et al. 2015). We allowed detection probability to vary by site, year, chick age, and the interaction of year and chick age. We expected detectability would increase with age, as younger chicks spend more time in interior habitats (Loefering and Fraser 1995) than on shorelines and may remain motionless or crouch in response to observers (Flemming et al. 1988, Colwell et al. 2007), and that the effect of age could vary by year based on the amount of vegetative cover available to conceal chicks or other sources of annual variation. Because the sandbars on NIO generally were smaller than sandbars on LCL, we expected higher detection rates on NIO compared to LCL.

Modeling was conducted in two steps: first, we developed baseline models for both survival and detection probability by modelling all possible subsets of year and age (linear and categorical), including additive and interactive effects. Next, we tested specific ecological hypotheses about survival by adding covariates for hatch date, natal site, and site-specific water flow to the best structure from step 1 (Appendix A). Prior to modeling, we used methods described by (Bishop et al. 2008) comparing empirical variances to simulated values to estimate

overdispersion (\hat{c}). We performed a single analysis with a fixed effect for site (NIO or LCL) to reduce uncertainty related to low sample size on NIO.

Adult survival and movement. We used multi-state mark-recapture models to estimate annual transition (ψ), apparent survival (ϕ), and detection (p) rates of adult (>1 year post-hatch) and hatch-year (“HY”, from hatch to 1 year old) plovers at NIO, LCL, and GVP. Transition rates were the inter-annual movement probabilities of adults among the study sites, i.e., emigration and immigration rates among NIO, LCL and GVP. Each year an individual bird was observed in the study area, we considered it a resident of one site (NIO, LCL, or GVP). We assigned individuals present at multiple sites in a year to one site in accordance with their breeding location. We assigned individuals with unknown breeding location to the site at which they were seen most frequently, or considered them unseen in that year if we found them an equal number of times at multiple locations (10 out of >20,000 occasions; Catlin et al. 2016). We assigned hatch-year birds to their natal site.

We undertook modeling in four successive steps to reduce the total number of models under consideration (Appendix B) and used the median \hat{c} test to estimate and correct for overdispersion. We developed the best general models for p , ϕ , and ψ (steps 1–3, respectively) to which we could add our specific ecological hypotheses about transition probability (step 4). First, we tested models where detection varied by age class, site, and survey effort, while survival and transition were held constant at their respective full models ($\phi_{\text{Site} + \text{Year} + \text{Age class} + \text{HY}(\text{Hatch} + \text{Banding})}$, $\psi_{\text{Site} \times \text{Year} + \text{Age class}}$). We expected that hatch-year birds would be less detectable than adults because they have a lower probability of breeding (Saunders et al. 2014) and may be less conspicuous if not defending eggs or chicks. We also expected detection variation based on site because of differences in sandbar size and vegetative cover, and based on survey effort level (2011–2014 or 2015–2016).

Second, we tested survival models while detection was held constant at the best model from step 1 and transition was held constant at its full model. We allowed survival to vary by age class, site, year, and the hatch date (standardized to 20 April = 0) and banding age of HY birds. We predicted that HY birds would have lower survival than adult birds, and that earlier hatch date and older age at banding would increase hatch-year survival (Catlin et al. 2015). We fixed HY survival and transition rates from GVP in 2011 at 0 because no chicks hatched in that year due to prolonged flooding.

Third, we tested models where transition probability varied by age class, site, and year, while detection and survival were held constant at their best models from steps 1 and 2, respectively. We expected that HY birds would have higher transition rates than adults based on established patterns of natal dispersal in piping plovers (Haig and Oring 1988a, Catlin et al. 2016), and that spatial and temporal factors, especially as regards habitat availability (described below) would contribute to transition probability.

In the final step, we examined the effect of amount of potential nesting habitat on transition rates. We added predictors for the effect of habitat area on transition probability to the top transition model from step 3, while detection and survival were held constant at their best models from steps 1 and 2, respectively. We hypothesized that, between years, plovers would move from sites with relatively low habitat area to sites with relatively high habitat area, i.e., we predicted birds would emigrate from site “A” to site “B” when the habitat area at site “A” in year $t+1$ was low relative to the average habitat area at any site in any year. Likewise, we predicted birds would immigrate to site “B” from site “A” when the habitat area at site “B” in year $t+1$ was high relative to the average amount of habitat area at any site in any year. Because of the observed decline in the Niobrara plover population, we were particularly interested in dispersal out of the Niobrara to LCL or GVP in response to habitat creation on those sites.

General modeling approach. We performed nest survival analyses with PROC NLMIXED in SAS (SAS Institute, Cary, NC) and capture-mark-recapture analyses in Program MARK (White and Burnham 1999) using the R (R Development Core Team 2017) package RMARK (Laake and Rexstad 2012). We evaluated support for models using an information-theoretic approach (Burnham and Anderson 2002) and Akaike's Information Criterion adjusted for sample size (AIC_c) and overdispersion (where necessary, $QAIC_c$). We considered covariate effects meaningful if 95% confidence intervals of β coefficients did not include 0 and if presence of a covariate improved the model fit, compared to a similar model without that covariate (Arnold 2010). For beta estimates, we provided estimates from the top-ranked model (Cade 2015). We standardized (mean = 0.0, SD = 1.0) all linear covariates in this analysis, which allowed for cross comparisons of relative effect sizes among variables. We presented means as mean \pm 1SD unless otherwise indicated.

Results

Nest survival

Niobrara River. We located 115 plover nests, with no nests found in 2013 or 2014. The number of nests per breeding season generally declined over the course of the study. Daily nest survival was negatively related to water flow ($\beta_{\text{flow}} = -0.76$, 95% CI = -1.16– -0.36; Figure 2, Table 1). At mean water flow, the nest daily survival rate was 0.955 ± 0.009 (mean \pm SE), and the probability that a nest would survive from initiation to hatching was 0.21 (95% CI: 0.11–0.38). Nest age, date, and clutch size were not supported as predictors of nest survival. Aside from the global model, all models that contained these variables ranked lower than the null model (Table 1). Apparent nest success was 27%, with two nests having indeterminate fates. Flooding (43%), unknown cause (30%), and depredation (13%) were primary causes of nest failure. The effect of year was non-significant in the global model ($F_{4, 38} = 1.03$, $P = 0.405$) and thus was not included

as a fixed effect in the analysis. The global model met assumptions of fit (Hosmer and Lemeshow test, $\chi^2 = 10.68$, $P = 0.221$, $N = 362$).

Lewis and Clark Lake. We monitored 521 nests and assessed nest fate at 503 nests. Daily nest survival was negatively related to water flow ($\beta_{\text{flow}} = -0.45$, 95% CI = -0.66– -0.24; Figure 2, Table 2). Daily nest survival (at mean water flow) varied by year (range: 0.913–0.982; Figure 3), and across years the probability that a nest would survive to hatching (0.23, 95% CI: 0.14–0.36) was similar to the Niobrara. Nest age, date, and clutch size were not supported as predictors of nest survival; aside from the global model, all models that contained these variables ranked lower than the null model (Table 2). Apparent nest success was 37%, and nest failure was due primarily to depredation (45%), unknown causes (45%), and flooding (5%). Apparent nest success was higher in 2014 (60%) than in any other year (range: 13%–41%). Year was significant as a fixed effect in the global model ($F_{4, 81} = 5.15$, $P = 0.001$), and thus was included in all models. The global model met the assumptions of fit (Hosmer and Lemeshow test, $\chi^2 = 9.34$, $P = 0.314$, $N = 2693$).

Chick survival

We banded 66 chicks on NIO and 465 chicks on LCL. Daily chick survival to fledging (25 days) was negatively associated with water flow, with a pronounced decline in survival once flows exceeded 1 SD over the mean (Figure 4), though the effect was significant only on the Niobrara River ($\beta_{\text{NIO:flow}} = -1.21$, 95% CI = -1.63– -0.79; $\beta_{\text{LCL:flow}} = -0.21$, 95% CI = -0.62–0.21). Survival at both sites was highest in 2010–2012 and declined from 2013–2016 (Figure 5). Site appeared in two competitive models ($\Delta\text{QAIC}_c \leq 4$; Table 3), and average apparent chick survival to fledging was higher on LCL (0.61 ± 0.01 ; mean \pm SE) than on NIO (0.54 ± 0.01 ; mean \pm SE), but exclusion of the site variable improved model fit (decreased QAIC_c by 1.33; Table 3). The best model containing hatch date was competitive, but effect size for this variable was relatively small and confidence limits overlapped 0 ($\beta_{\text{Hatch}} = -0.01$, 95% CI = -0.02–0.01). Age at banding was not an important predictor of survival. Detection probability varied by age (categorical) and year (Table 3) and was higher on NIO than LCL ($\beta_{\text{NIO}} = 2.02$, 95% CI = 1.49–2.55; Table 2). There was minimal overdispersion ($\hat{c} = 1.08$).

Adult and hatch-year survival

We observed 1,874 unique adult and hatch-year plovers across the three study sites. Apparent annual survival was higher for adults (0.76 ± 0.01 ; mean \pm SE) than HY birds (0.27 ± 0.02 ; mean \pm SE). Survival generally increased by year for both age classes (Figure 6), with lowest rates during and immediately after Missouri River flooding (2011–2013) followed by higher rates from 2013–2016. There was a positive relationship between age at banding and survival of HY birds ($\beta_{\text{Banding}} = 0.17$, 95% CI = 0.02–0.33) and a negative relationship between hatch date and survival of HY birds ($\beta_{\text{Hatch}} = -0.37$, 95% CI = -0.53– -0.20). The median \hat{c} test indicated minimal overdispersion ($\hat{c} = 1.07$).

Site did not appear in the top-ranked survival model from step 2, but it was present in a competing model ($\Delta\text{QAIC}_c = 1.55$; Appendix C, row 13). Estimates from this model suggest higher adult and hatch-year survival on NIO (adult: 0.82 ± 0.03 , hatch-year: 0.41 ± 0.06 ; mean \pm SE) compared to LCL (adult: 0.76 ± 0.02 SE, hatch-year: 0.32 ± 0.03 ; mean \pm SE) or GVP (adult: 0.76 ± 0.02 , hatch-year: 0.34 ± 0.03 mean \pm SE), but relatively small sample sizes on NIO may have led to lower ranking for that model. Across all sites, adults were detected at a higher rate (0.72 ± 0.03 ; mean \pm SE) than HY birds (0.49 ± 0.03 ; mean \pm SE). Detection probability was higher (0.96 ± 0.01 ; mean \pm SE) on GVP when survey frequency was higher (2011–2014) compared to when surveys were less frequent (2015–2016, 0.47 ± 0.05 ; mean \pm SE).

Adult and hatch-year movement

Of the 1,874 banded individuals, 59 adult and 66 hatch-year birds were banded or first detected on NIO, 403 adult and 377 HY birds on LCL, and 227 adult and 742 HY birds on GVP. The area of potential plover nesting habitat (open to sparsely vegetated dry or wet sand) was 1636 ± 123 ha (range: 1525–1837) on NIO, 1392 ± 820 ha (range 856–2800) on LCL, and 1449 ± 369 ha (range: 1108–2040) on GVP. At each of the three sites, the habitat area generally decreased over time. Habitat area was positively correlated among the sites (all $r \geq 0.96$).

The amount of potential nesting habitat at a site affected adult and hatch-year transition rates differently (Table 4, Figure 7). Increasing habitat area at a site had a marginal negative effect on HY emigration from that site ($\beta_{\text{HY habitat emigration}} = -0.34$, 95% CI = -0.75 – 0.08). Conversely, increasing habitat area at a site was positively related to adult emigration from that site ($\beta_{\text{Adult habitat emigration}} = 0.19$, 95% CI = 0.07 – 0.30). Several competing models ($\Delta\text{AIC}_c < 2$) included the effect of habitat availability on immigration to a site, but inclusion of the variable did not improve model fit (Table 4).

Hatch-year birds had a higher transition rate (0.18 ± 0.03 , mean \pm SE) than adult birds (0.09 ± 0.01 , mean \pm SE) across all sites ($\beta_{\text{Age}} = 1.27$, 95% CI = 0.80 – 1.75). Plovers of both age classes transitioned from NIO to LCL at the highest rates and from GVP to NIO at the lowest rates (Figure 8). Transition rate did not appear to vary by year; the highest model containing year received no model weight (Appendix C, row 8).

Discussion

Piping plover nest and chick survival rates were highest at low river flow on both the Niobrara River and Lewis and Clark Lake. However, flooding was a greater source of nest and chick mortality on the Niobrara. Nearly half of all NIO nest failures resulted from inundation, compared to only 5% on LCL. The relative effect size of flow on nest survival at each site (NIO β 1.7 times greater than LCL) underscored this difference. Likewise, the effect of flow on chick survival was 5.8 times greater on NIO than LCL. Direct flood-related chick mortality is difficult to document, but can be inferred when chicks disappear from recently overwashed sandbars; this was observed on NIO but not LCL. The relative effect of flow on the Niobrara compared to Lewis

and Clark Lake indicates that similar increases in flow at the two sites did not similarly affect survival rates or sandbar inundation at the two sites.

Sandbars that are low in elevation relative to water level are susceptible to inundation. Fine-scale elevation data were not available for this study, but the strong effect of even moderate flow increases on nest and chick survival rates provides support that sandbar nesting habitat on the Niobrara was relatively low elevation. We found that flow increases 1 SD above average reduced the probability of nest success or chick survival by more than half on NIO. Chick survival was somewhat more robust to water flow than nest survival, presumably because mobile chicks were able to move to higher elevation area of sandbars during periods of high flow.

Lewis and Clark Lake sandbars were high in elevation relative to water level (Johnson et al. 2015), yet increased flows still negatively affected nest and chick survival. The rarity of flood-caused mortality (i.e., eggs or chicks washed away during increased water flow) suggests that water flow on LCL did not affect survival directly. Even at levels insufficient to inundate nesting habitat, increased flow during the breeding season can negatively impact piping plovers by encroaching on the periphery of sandbars and reducing total sandbar area (Espie et al. 1998). Increased water flow is linked to slower weight gain in plover chicks and longer time to fledging (Catlin et al. 2013), a possible result of food limitation caused by submersion of the prey-rich saturated and moist substrates on which piping plover chicks preferentially forage (Le Fer et al. 2008). Decreased nest and chick survival at higher flows also may have resulted from negative density-dependent processes, including increased intra- and interspecific competition and predation. (Hunt et al. 2018) found substantially higher predation rates of piping plover nests and chicks in high density compared to low density years, likely due to increased predator efficiency over a smaller search area (Kruse et al. 2001, Claassen 2004, Catlin et al. 2013). Rising water levels could increase competition for space, and push nesting territories into areas that are higher-elevation, but suboptimal in other aspects (e.g., closer to dense vegetation (Cohen et al. 2009) or in a less suitable substrate (Espie et al. 1996, Anteau et al. 2012)). These indirect effects of increased water flow were likely responsible for diminished nest and chick survival on both NIO and LCL, but direct flood-related mortality appeared to occur nearly exclusively on NIO.

Survival rates of nests, chicks, and adults generally were comparable between the Niobrara River and Lewis and Clark Lake, yet we found an overall decline in use of the Niobrara while the regional population remained stable (Andres et al. 2012, Hunt et al. 2018). This suggests that low survival and reproductive output were not primarily responsible for the Niobrara population decline. Over the course of the study, we observed a high (>50%) probability of dispersal from NIO to LCL between breeding seasons. There was little exchange between NIO and the Gavins Point Reach, potentially due to the distance between those sites

(Catlin et al. 2016). We predicted emigration would be negatively related to habitat area and immigration would be positively related to habitat area. Namely, we expected plovers would disperse from the Niobrara as sandbar area on Missouri River sites increased substantially following historic flooding 2010–2011 and created a potential for population growth (Catlin et al. 2015, Hunt et al. 2018). We did not find a temporal effect on dispersal, but age class and habitat availability did influence movement rates in ways that provide some support for this hypothesis. Overall, we found that hatch-year birds dispersed at higher rates than adults. Hatch-year birds moved from their natal sites, especially the Niobrara, at high rates, in keeping with the established pattern of natal dispersal in piping plovers (Haig and Oring 1988b). The probability of hatch-year dispersal increased when habitat availability was relatively low at the natal site. Hatch-year birds may exhibit higher natal site fidelity when habitat is abundant, likely in response to decreased competition for space with older, more experienced breeders (Catlin et al. 2015). Breeding in a familiar area may confer advantages to fitness such as known foraging locations (Davies and Houston 1981) and predator communities (Yoder et al. 2004) as well as established relationships with neighbors (Krebs 1982).

Dispersal probability of adult birds, on the contrary, increased when habitat availability at their breeding site was high relative to the average amount in this study. Habitat availability across sites was correlated and was highest in 2012, generally decreasing over time. The pattern of emigration from sites with relatively abundant habitat may reflect the amount of movement that occurred during and following widespread Missouri River flooding in 2011 (Catlin et al. 2016). Dispersals from 2010–2011 were not a part of this study because we did not band birds on the Niobrara in 2010, but many (15/39) of the banded adults on NIO in 2011 were known LCL or GVP residents in previous years. Of these individuals, all 5 that were known to survive past 2011 returned to their original breeding site. Complete submersion of GVP habitat increased nesting density on LCL in 2011 (Catlin et al. 2016) and may have instigated temporary (1 breeding season) movement to the Niobrara. The high rate of emigration that we observed from NIO is due in part to subsequent return of these individuals to LCL or GVP when habitat again became available, and emphasizes the role of NIO in supporting Missouri River birds when habitat availability decreases on the Missouri (Adolf et al. 2001).

Differences in relative habitat quality between the Niobrara and Lewis and Clark Lake may have contributed to relatively high emigration rate from the Niobrara. Area of open to sparsely vegetated wet and dry sand is considered an appropriate estimate of habitat abundance on the Missouri River (Catlin et al. 2011, Hunt et al. 2018), though plovers largely choose dry substrate over wet. Sandbar habitat on GVP and LCL was dominated by dry sand, while NIO sandbars were only 45–60% dry sand. Plovers may have emigrated from the Niobrara, even in years when habitat area was relatively high there, because much of the habitat was wet sand, and therefore potentially lower quality. Site fidelity is generally high in

plovers (83–94%; Cohen et al. 2006, LeDee et al. 2010, Cohen and Gratto-Trevor 2011, Catlin et al. 2015), but habitat quality is linked to emigration (Cohen et al. 2006). Previous research on Lewis and Clark Lake found high rates of chick growth (Catlin et al. 2014), chick survival, and reproductive output (Catlin et al. 2015), indicating that it was high-quality plover nesting and brood-rearing habitat. Plovers may have emigrated to newly created sandbars on Lewis and Clark Lake because the habitat was more suitable for nesting and brood-rearing than Niobrara River sandbars.

Breeding dispersal is a common response to reproductive failure in birds (Greenwood and Harvey 1982, Part and Gustafsson 1989, Haas 1998, Daniels and Walters 2000, Catlin et al. 2005), including piping plovers (Roche et al. 2012, Friedrich et al. 2014). The high probability of dispersal that we observed from the Niobrara could have been related to the high rate of nest failure, and the cause of nest failure. In Manitoba, plovers dispersed farther and more often following flooding-caused nest failure than following nest depredation (Haig and Oring 1988b). Roche et al. 2012 found an effect of flooding on breeding dispersal even in reproductively successful plovers. The high dispersal rate of adults that we observed on the Niobrara River could be a response to flooding, particularly repeated flooding in high-water years.

Conservation Implications

Low nest and chick survival and high emigration contributed to population decline on the Niobrara 2010–2016. Increases in river flow had strong negative effects on reproductive success, and may have been a contributing factor in the high dispersal rate to Lewis and Clark Lake. Flooding is a natural event on unregulated rivers (Sidle et al. 1992), but the strong effect of river flow on nest and chick survival on the Niobrara suggests that plovers may have face more frequent and intense levels of breeding season flooding than is typical. Since construction of mainstem Missouri River dams in the mid-1950s, the Niobrara has evolved from a relatively deep, stable channel to a relatively shallow, aggrading channel (Skelly et al. 2003). Concurrently, average spring and summer streamflow in the lower Niobrara has increased (Norton et al. 2014) and there is an increase in the frequency and intensity of storms in the central U.S. (Kunkel et al. 2012, Feng et al. 2016). The upstream effects of dams along with increases in streamflow (Norton et al. 2014) and precipitation (Kunkel et al. 2012) pose a continued threat of flooding and habitat loss to sandbar nesting birds on the Niobrara River. Sediment deposition at the Niobrara-Missouri confluence is expected to eventually extend farther upstream on the Niobrara River and downstream on the Missouri River towards the Gavins Point Dam (Skelly et al. 2003), which may affect an even greater portion of the regional plover population.

Local population declines of species that occupy successional habitats are expected; as habitat develops and becomes unsuitable for the species in an area, individuals may move to areas of suitable habitat (Newton 1998). The regional interchange among subpopulations when

habitat is higher-quality at one site compared to another has been noted previously in plovers (Catlin et al. 2016), including between the Niobrara and Missouri rivers (Adolf et al. 2001). During this study, the Niobrara plover population declined as both hatch-year and adult birds moved from the Niobrara to Lewis and Clark Lake coincident with expansive habitat creation on the Missouri River. As sandbars age, the quantity and quality of plover nesting habitat are reduced through erosion and vegetation encroachment. Chick survival, and to a lesser degree nest survival, have declined since habitat was created on Lewis and Clark Lake. As habitat on Lewis and Clark Lake ages and becomes less suitable, ensuring alternate sources of habitat, like the Niobrara, is important for sustaining the regional population (Zeigler et al. 2017). Understanding ecological effects of reservoir sedimentation on upstream tributaries is integral to management decisions regarding conservation value of sedimentary deltas.

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Tables

Table 1. Model rankings for a random effects logistic exposure model of piping plover nest survival on the Niobrara River, NE (2010–2012, 2015–2016).

Model ^a	k ^b	ΔAIC_c^c	Likelihood	Weight
Sandbar × Year + Flow	3	0.00	1.00	0.79
Sandbar × Year + Flow + Age + Date + Clutch	6	2.60	0.27	0.21
Sandbar × Year	2	20.9	0.00	0.00
Sandbar × Year + Age	3	22.0	0.00	0.00
Sandbar × Year + Date + Clutch	4	22.4	0.00	0.00
Sandbar × Year + Age + Date	4	23.1	0.00	0.00

^a Nest survival rate varied by: Flow – maximum daily water flow (m^3/s) during a visit interval, Age – age in days of a nest at the mid-point of the visit interval, Date – day of year standardized to 20 April = 0, Clutch – number of eggs in a nest at the start of the visit interval, and Sandbar × Year – a random effect of annual, sandbar-specific variation. All linear covariates were standardized (mean = 0.0, SD = 1.0). All models include an intercept.

^b Number of parameters in the model.

^c Akaike's Information Criterion corrected for small sample size. Minimum $AIC_c = 302.7$.

Table 2. Model ranking results for a random effects logistic exposure model of piping plover nest survival on the Lewis and Clark Lake segment of the Missouri River, NE/SD (2012–2016).

Model^a	k^b	ΔAIC_c^c	Likelihood	Weight
Sandbar × Year + Year + Flow	7	0.00	1.00	0.94
Sandbar × Year + Year + Flow + Age + Date + Clutch	10	5.60	0.06	0.06
Sandbar × Year + Year	6	19.6	0.00	0.00
Sandbar × Year + Year + Age	7	21.2	0.00	0.00
Sandbar × Year	2	21.7	0.00	0.00
Sandbar × Year + Year + Age + Date	8	23.0	0.00	0.00
Sandbar × Year + Year + Date + Clutch	8	23.1	0.00	0.00

^a Nest survival rate varied by: Flow – maximum daily water flow (m) during a visit interval, Age – age in days of a nest at the mid-point of the visit interval, Date – day of year standardized to 20 April = 0, Clutch – number of eggs in a nest at the start of the visit interval, Year – 2012–2016 (categorical), and Sandbar × Year – a random effect of annual, sandbar-specific variation. All linear covariates were standardized (mean = 0.0, SD = 1.0). All models include an intercept.

^b Number of parameters in the model.

^c Akaike’s Information Criterion corrected for small sample size. Minimum AIC_c = 1909.2.

Table 3. Model ranking results for a Cormack-Jolly-Seber model of survival (ϕ) and detection probability (p) of pre-fledge piping plover chicks on the Niobrara River, NE and the Lewis and Clark Lake segment of the Missouri River, NE/SD (2010–2016).

ϕ^a	p^b	k^c	$\Delta QAIC_c^d$	Weight
Year + NIO:flow + LCL:flow	age \times Year + Site	185	0.00	0.38
Year + NIO:flow + LCL:flow + Hatch	age \times Year + Site	186	0.91	0.24
Year + NIO:flow + LCL:flow + Hatch + Site	age \times Year + Site	187	1.33	0.19
Year + NIO:flow + LCL:flow + Site	age \times Year + Site	186	1.48	0.18

^a Survival rate varied by: Age – age of a chick in days since hatch (linear), age – age of a chick in days since hatch (categorical), Year – a categorical variable for year (2010–2016), Hatch – hatch date (standardized to 20 April = day 0), Site – Niobrara River or Lewis and Clark Lake, NIO:flow – daily maximum water flow (m^3/s) on the Niobrara River, and LCL:flow – daily maximum water gage flow (m) on Lewis and Clark Lake.

^b Detection probability was predicted to vary by: Age – age of a chick in days since hatch (linear), age – age of a chick in days since hatch (categorical), Year – a categorical variable for year (2010–2016), and Site – Niobrara River or Lewis and Clark Lake.

^c Number of parameters in the model.

^d Akaike's Information Criterion corrected for small sample size and overdispersion ($\hat{c} = 1.08$). Only models with $\Delta AIC_c \leq 4$ are shown. Minimum $AIC_c = 4739.55$.

Table 4. Model ranking results for a multi-state mark-recapture model of transition (ψ) and survival (ϕ) rates of adult and hatch-year piping plovers on the Niobrara River, NE and the Gavins Point Reach and Lewis and Clark Lake segments of the Missouri River, NE/SD (2011–2016).

ψ^a	ϕ^b	k^c	$\Delta QAIC_c^d$	Weight	Deviance
Age + Site + Age \times Habitat _{Emigration}	Age + Year + Banding + Hatch	24	0.00	0.34	5102.91
Age + Site + Habitat _{Emigration} + Habitat _{Immigration}	Age + Year + Banding + Hatch	24	0.58	0.25	5103.49
Age + Site + Habitat _{Emigration}	Age + Year + Banding + Hatch	23	0.71	0.24	5105.66
Age + Site + Age \times (Habitat _{Emigration} + Habitat _{Immigration})	Age + Year + Banding + Hatch	26	1.85	0.13	5100.70

^a Transition rate was predicted to vary by: Age – hatch-year (1 year post-hatch) or adult (>1 year post-hatch), Habitat_{Emigration} – the area of potential nesting habitat at a site affects the emigration rate from that site, Habitat_{Immigration} – the area of potential nesting habitat at a site affects the immigration rate to that site, Site – Gavins Point Reach, Lewis and Clark Lake, or Niobrara River, and Year – 2011–2016.

^b Survival rate was predicted to vary by: Age – hatch-year (1 year post-hatch) or adult (>1 year post-hatch), Year – 2011–2016, Banding – age in days at banding (affected hatch-year birds only), Hatch – hatch date standardized to 20 April = 0 (affected hatch-year birds only), and Site – Niobrara River, Gavins Point Reach, or Lewis and Clark Lake.

^c Number of parameter in the model.

^d Akaike’s Information Criterion corrected for small sample size and overdispersion ($\hat{c} = 1.07$). Only models with $\Delta QAIC_c \leq 4$ are shown. The model structure for detection probability ($p_{\text{Site} \times \text{Survey effort} + \text{Age class}}$) was consistent for all models shown. Survey effort is a binary variable representing different monitoring intensity depending on level of bird activity and project focus (pre-2015 or post-2015). Minimum QAIC_c = 5151.33.

Figures

Figure 1. Map of study site locations along the Missouri and Niobrara rivers. The Niobrara River study site is indicated by a crosshatched background; the Gavins Point Dam separates the upstream Lewis and Clark Lake segment (stippled background) from the downstream Gavins Point Reach segment (hatched background) of the Missouri River. Inset map shows the location of the study area and the Great Plains breeding range of the piping plover within North America.

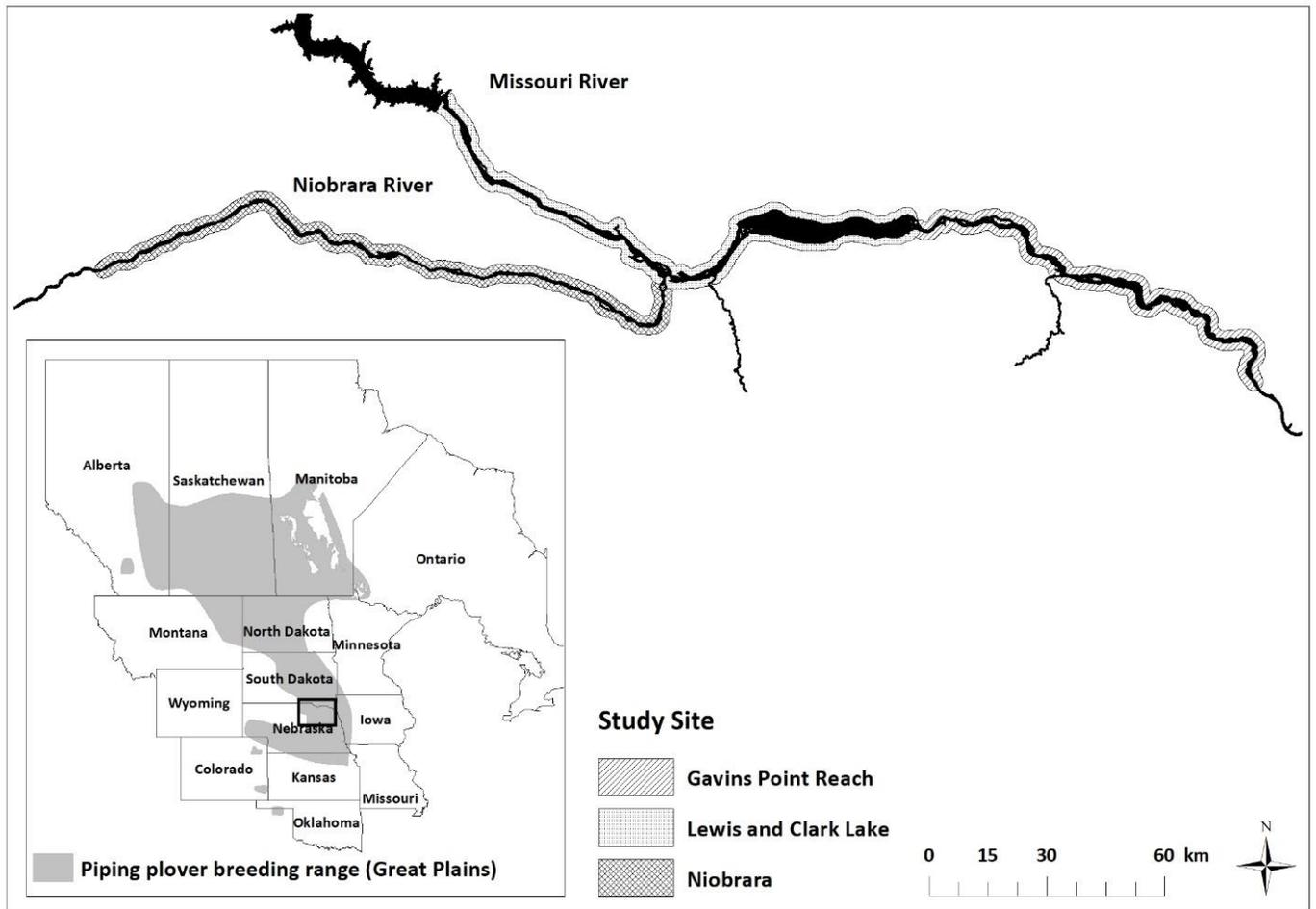


Figure 2. Predicted probability of piping plover nest success in relation to water flow on the Niobrara River, NE (NIO; dashed line) and Lewis and Clark segment of the Missouri River, NE/SD (LCL; solid line), 2010–2016. Water flow was standardized (mean = 0.0, SD = 1.0) and scaled by site (NIO mean \pm SD: 126 \pm 97 m³/s, range: 25–479 m³/s; LCL mean \pm SD: 6.25 \pm 0.20 m, range: 5.32–6.55 m). Estimates were derived from the top-ranked logistic exposure models, which contain a variable for water flow, a random effect of sandbar and year, and a fixed effect for year (LCL only). Shaded areas represent 95% confidence intervals.

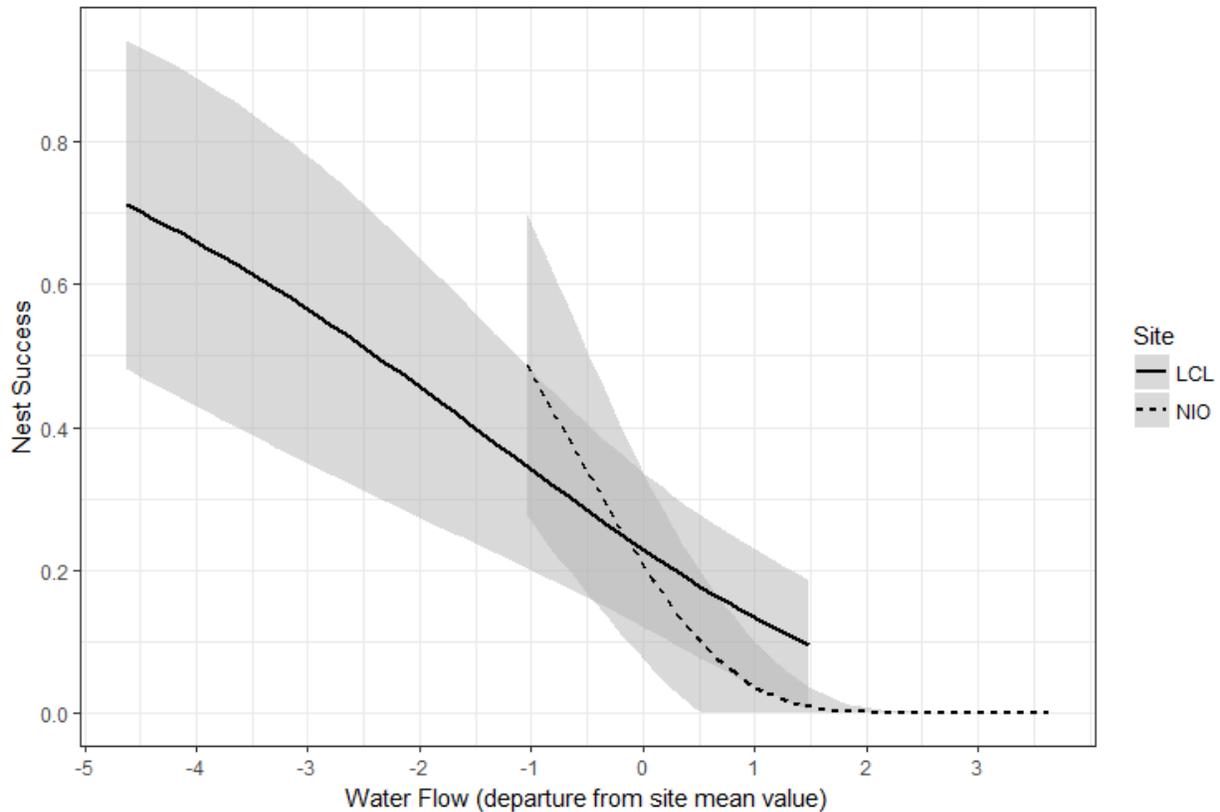


Figure 3. Daily survival rate of piping plover nests on the Lewis and Clark Lake segment of the Missouri River, NE/SD at mean water flow, 2012–2016. Estimates were derived from the top-ranked logistic exposure model, which contained variables for water flow, year, and a random effect of sandbar and year. Error bars represent 95% confidence intervals.

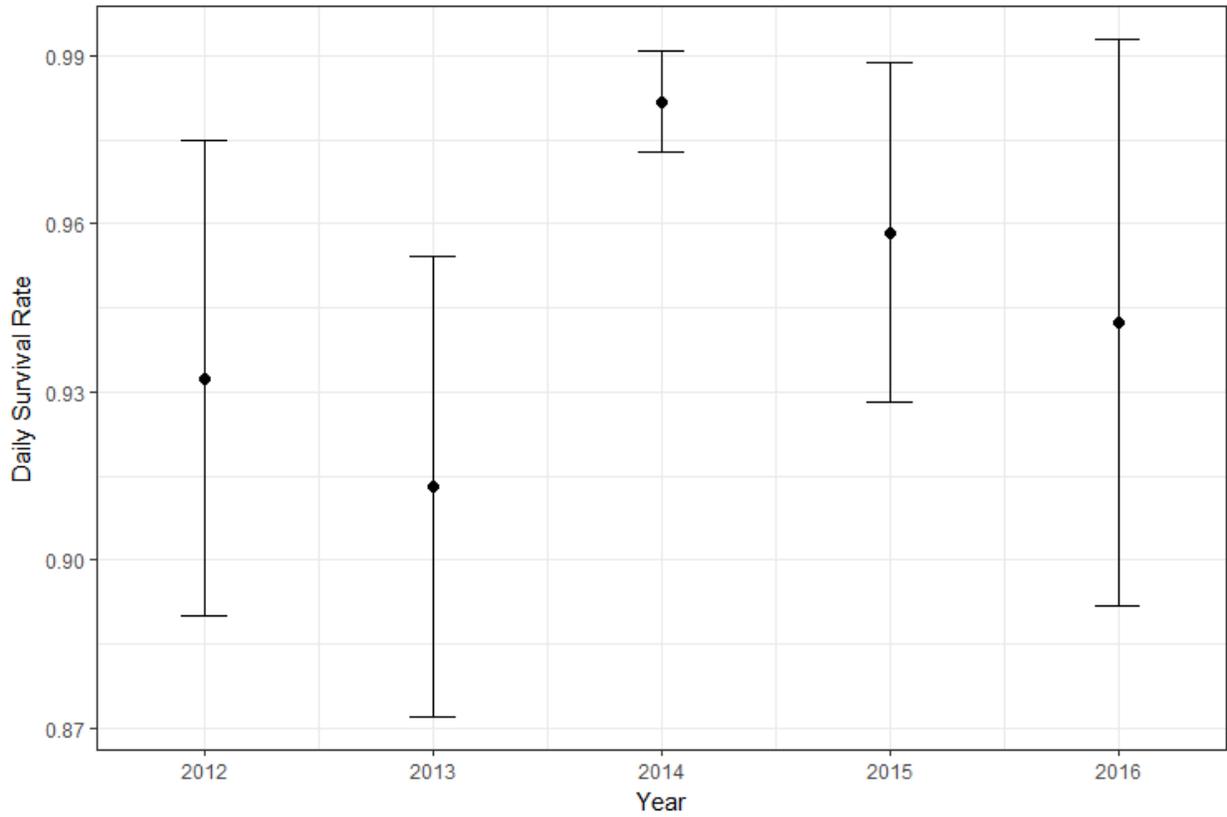


Figure 4. Predicted daily probability of pre-fledge (hatch to 25 days) chick survival for piping plovers in relation to water flow on the Niobrara River, NE (NIO; dashed line) and the Lewis and Clark segment of the Missouri River, NE/SD (LCL; solid line). Water flow was standardized (mean = 0.0, SD = 1.0) and scaled by site (NIO – $61 \pm 33 \text{ m}^3/\text{s}$, range: 20.5–284 m^3/s ; LCL – $6.74 \pm 0.89 \text{ m}$, range: 4.76–8.88 m). Estimates are from the top ranked Cormack-Jolly-Seber model and controlled for age, year (2015), and hatch date. Shaded areas represent 95% confidence intervals.

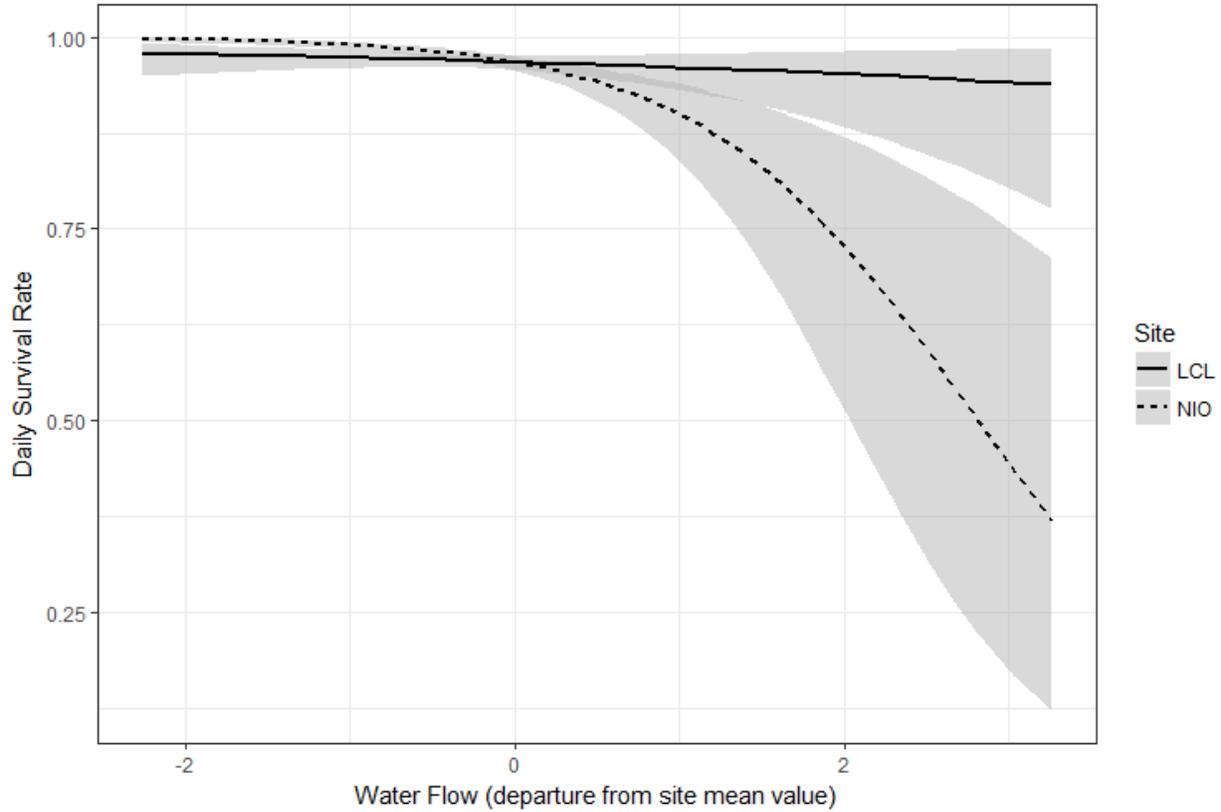


Figure 5. Annual cumulative survival of pre-fledge piping plovers (hatch to 25 days) on the Niobrara River, NE (NIO; closed circles) and the Lewis and Clark segment of the Missouri River, NE/SD (LCL; open circles). On NIO, piping plover chicks were not banded in 2010 and there were no nests in 2013–2014. Estimates and standard errors are derived from model-averaged parameter estimates and unconditional standard errors of daily survival using the delta method (Powell 2007). Error bars represent 95% confidence intervals.

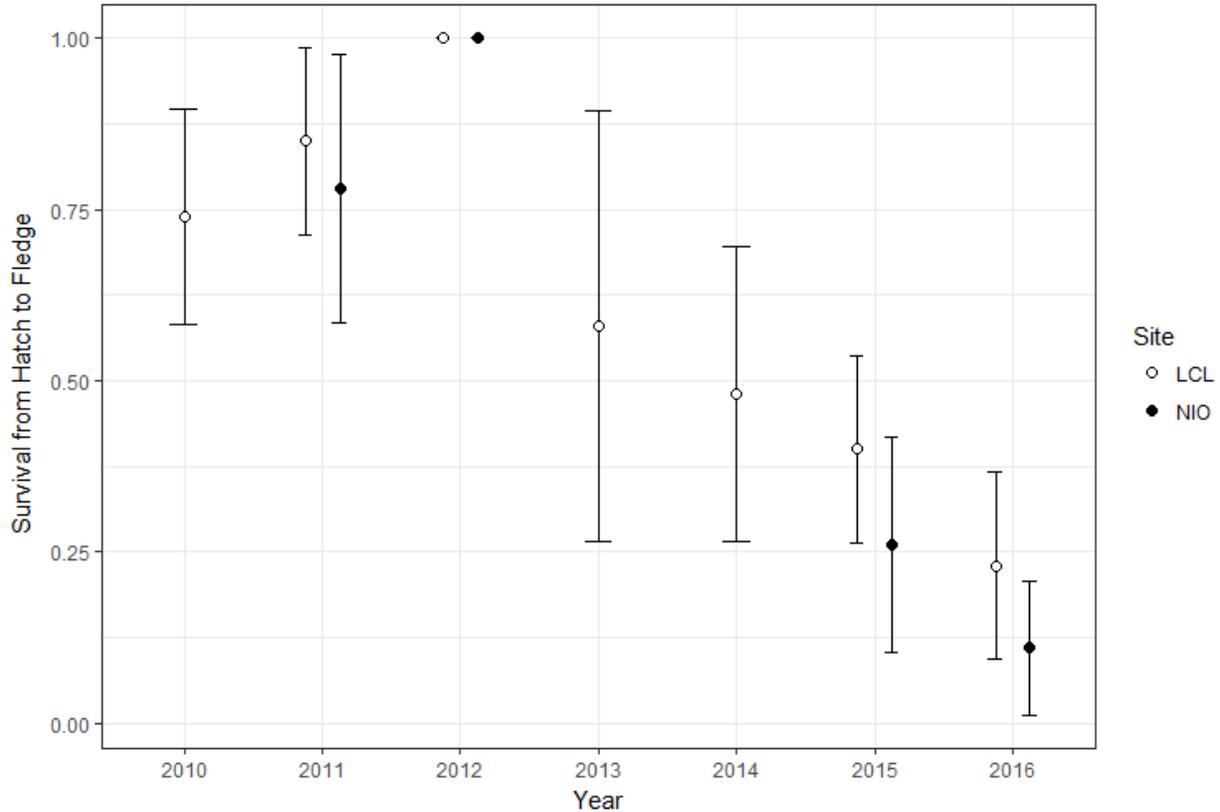


Figure 6. Apparent survival (ϕ) rates of adult (open circle; >1 year post-hatch) and hatch-year (closed circle; 1 year post-hatch) piping plovers on the Niobrara River, NE (NIO; dot-dashed error bar), the Gavins Point Reach segment of the Missouri River (GVP; dotted error bar), NE/SD, and the Lewis and Clark Lake segment of the Missouri River, NE/SD (LCL; solid error bar), 2011–2016. Estimates represent survival between successive breeding seasons and are derived from model-averaged parameter estimates from a multi-state mark-recapture model. Error bars represent 95% confidence intervals.

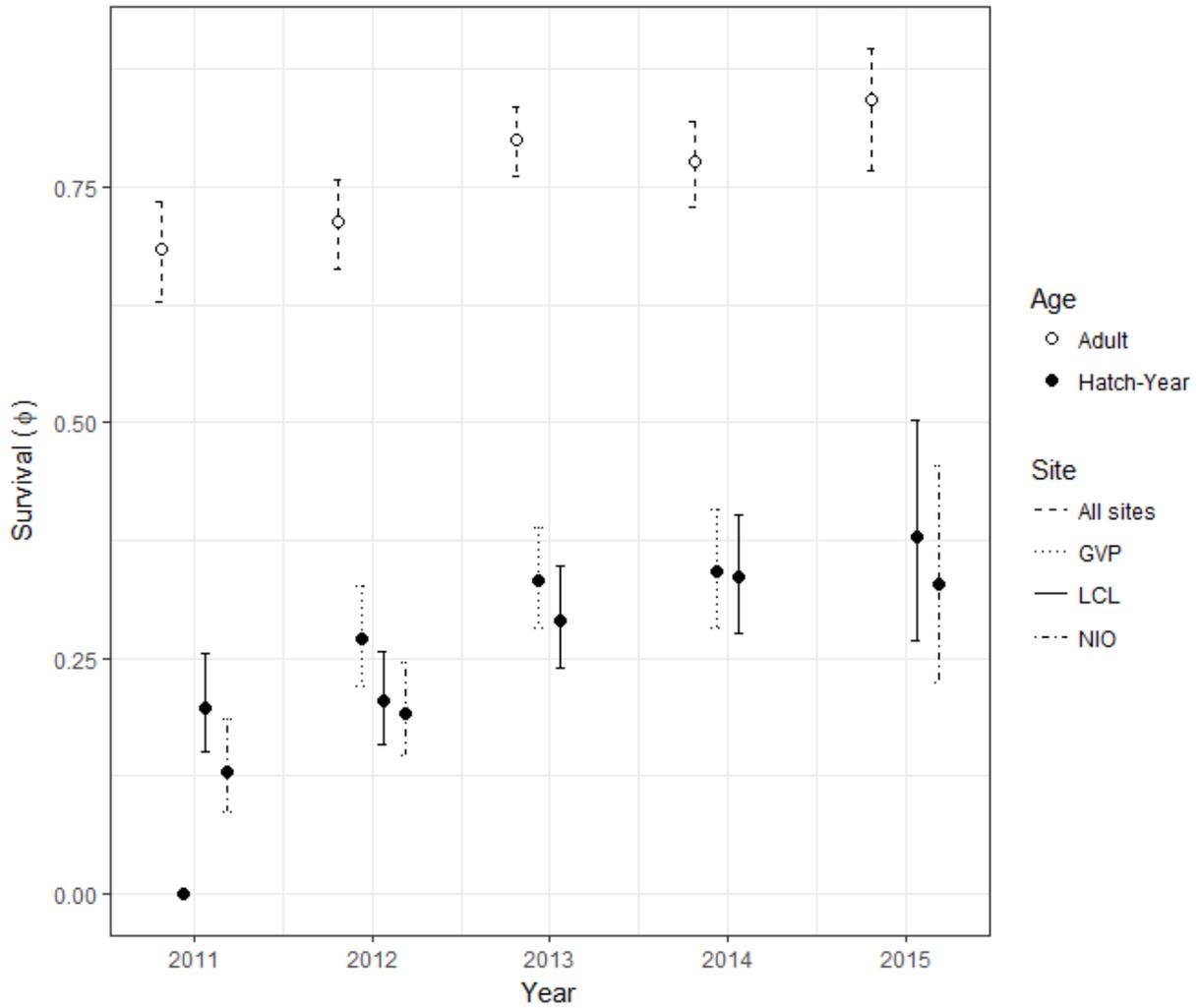


Figure 7. Predicted emigration rates of adult (solid line; >1 year post-hatch) and hatch-year (dashed line; 1 year post-hatch) piping plovers from the Niobrara River, NE to the Lewis and Clark Lake segment of the Missouri River, NE/SD in relation to area of potential nesting habitat (open to sparsely vegetated wet and dry sand) on the Niobrara River, 2011–2016. Estimates represent movement between successive breeding seasons and are derived from the top-ranked multi-state mark-recapture model. Shaded areas represent 95% confidence intervals.

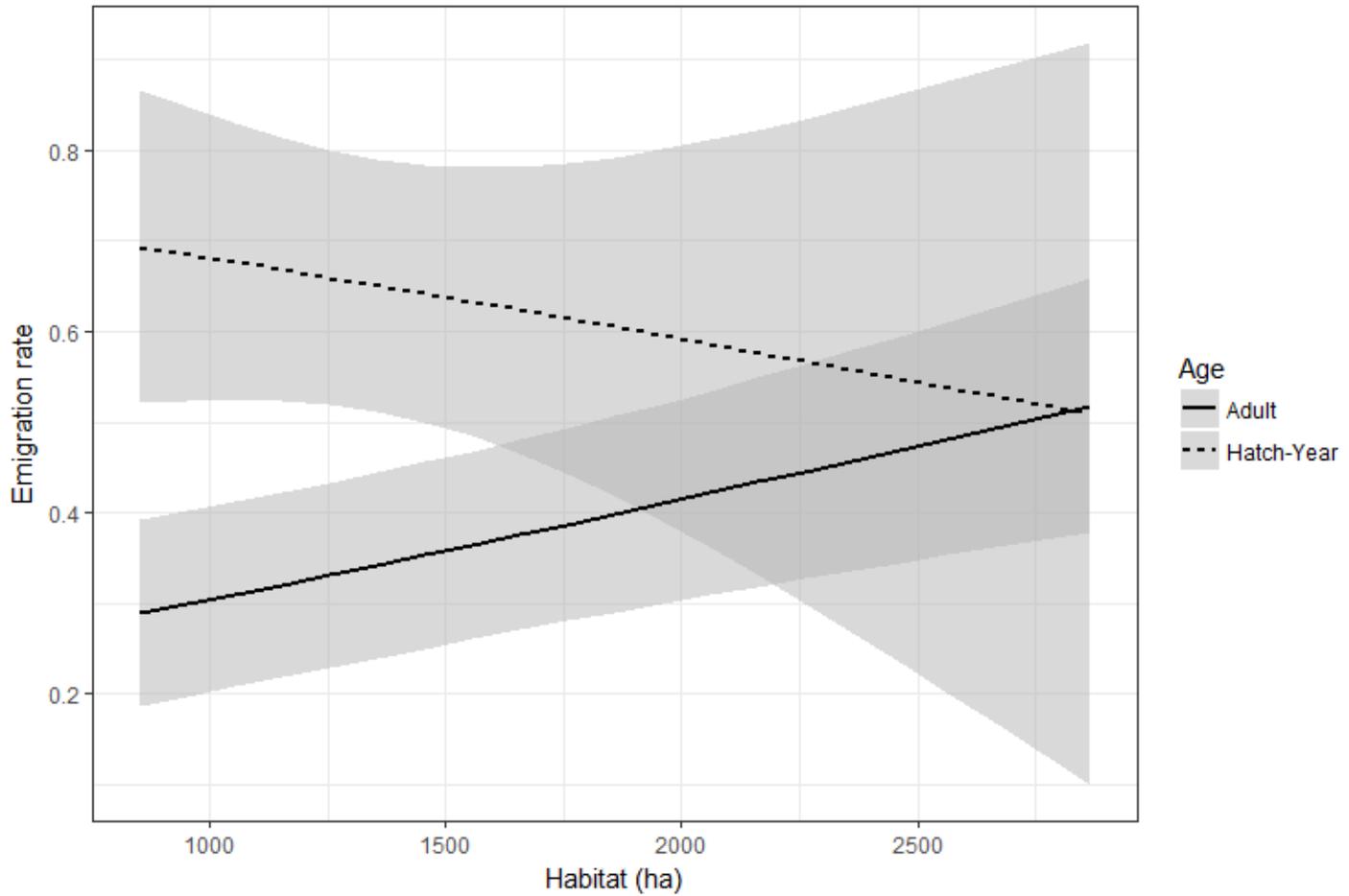
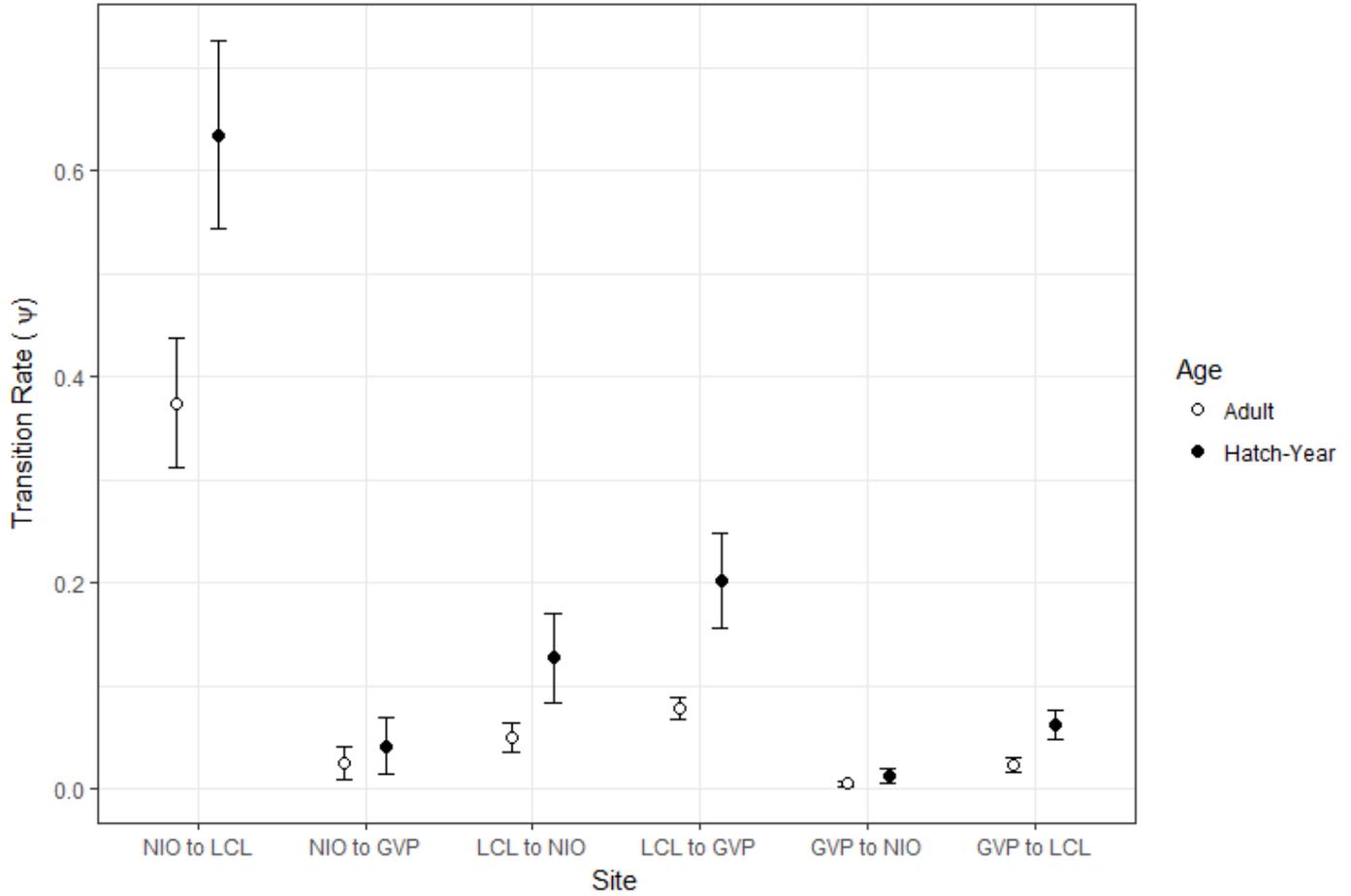


Figure 8. Transition (ψ) rates of adult (open circle; >1 year post-hatch) and hatch-year (closed circle; 1 year post-hatch) piping plovers among the Niobrara River, NE (NIO), the Gavins Point Reach segment of the Missouri River, NE/SD (GVP), and the Lewis and Clark Lake segment of the Missouri River, NE/SD (LCL), 2011–2016. Estimates represent movement from one site to another site in successive breeding seasons and are derived from model averaged parameter estimates from a multi-state mark-recapture model. Error bars represent 95% confidence intervals.



Supplemental Material

Appendix A. Definitions of basic model structures for model parameters apparent survival (ϕ) and detection (p) rate for pre-fledge piping plover chicks on the Niobrara River, NE and Lewis and Clark Lake Segment of the Missouri River, NE/SD (2011–2016).

Step	Parameter	Structure(s)	Definition
1	ϕ, p	Year	Year specific estimates
		Age	Age specific (linear trend) estimates
		Age + Year	Age (linear trend) and year specific estimates, additive effect of year
		Age \times Year	Age (linear trend) and year specific estimates, multiplicative effect of year
		age	Age specific (categorical trend) estimates
		age + Year	Age (categorical trend) and year specific estimates, additive effect of year
		age \times Year	Age (categorical trend) and year specific estimates, multiplicative effect of year
		.	Constant
2	ϕ	Best ₁	Best structure from Step 1
		Best ₁ + Hatch	Best structure from Step 1, additive effect of hatch date
		Best ₁ + Site	Best structure from Step 1, additive effect of site
		Best ₁ + NIO:flow + LCL:flow	Best structure from Step 1, additive effect of site-specific water flow
		Best ₁ + Hatch + Site	Best structure from Step 1, additive effects of hatch date and site
		Best ₁ + Hatch + NIO:flow + LCL:flow	Best structure from Step 1, additive effects of hatch date and site-specific water flow
		Best ₁ + Site + NIO:flow + LCL:flow	Best structure from Step 1, additive effects of site and site-specific water flow
		Best ₁ + Hatch + Site + NIO:flow + LCL:flow	Best structure from Step 1, additive effects of hatch date, site, and site-specific water flow
Best ₁ + Hatch \times Site + NIO:flow + LCL:flow	Best structure from Step 1, multiplicative effect of hatch date, additive effects of site and site-specific water flow		

Appendix B. Definitions of basic model structures for multi-state model parameters transition (ψ), survival (ϕ), and detection (p) rates for adult (>1 year post-hatch) and hatch-year (“HY”; 1 year post-hatch) piping plovers on the Niobrara River, NE and the Lewis and Clark Lake and Gavins Point Reach segments of the Missouri River, NE/SD (2011–2016).

Step	Parameter	Structure(s)	Definition
1	ϕ	Site + Year + Age class + HY(Banding + Hatch)	Site, year, and age (HY or adult) specific estimates, HY survival affected by age at banding and hatch date
		ψ	Site, year, and age specific estimates (full model)
	p	Site	Site specific estimates
		Site + Survey effort	Site and survey effort specific estimates, additive effect of survey effort
		Site \times Survey effort	Site and survey effort specific estimates, multiplicative effect of survey effort
		Site + Age class	Site and age specific estimates, additive effect of age
		Site + Age class + Survey effort	Site and age specific estimates, additive effects of age and survey effort
		Site \times Survey effort + Age class	Site, age, and survey effort specific estimates, additive effect of age, multiplicative effect of survey effort
2	p	Best ₁	Best structure from Step 1 ($p_{\text{Site} \times \text{Survey effort} + \text{Age class}}$)
	ψ	Site \times Year + Age class	Site, year, and age specific estimates (full model)
	ϕ	Site + Year + Age class + HY(Banding + Hatch)	Site, year, and age (HY or adult) specific estimates, HY survival affected by age at banding and hatch date
		Site + Age class + HY(Banding + Hatch)	Site and age (HY or adult) specific estimates, HY survival affected by age at banding and hatch date
		Year + Age class + HY(Banding + Hatch)	Year and age (HY or adult) specific estimates, HY survival affected by age at banding and hatch date
Age class + HY(Banding + Hatch)	Age (HY or adult) specific estimates, HY survival affected by age at banding and hatch date		
3	p	Best ₁	Best structure from Step 1 ($p_{\text{Site} \times \text{Survey effort} + \text{Age class}}$)

	ϕ	Best ₂	Best structure from Step 2 ($\phi_{\text{Year} + \text{Age class} + \text{HY}(\text{Banding} + \text{Hatch})}$)
	ψ	Age class	Age specific estimate
		Year	Year specific estimates
		Age class + Year	Age and year specific estimates, additive effect of year
		Site	Site specific estimates
		Site + Year	Site and year specific estimates, additive effect of year
		Site \times Year	Site and year specific estimates, multiplicative effect of year
		Site + Age class	Site and age specific estimates, additive effect of age
		Site + Year + Age class	Site, year, and age specific estimates, additive effects of year and age class
		Site \times Year + Age class	Site, year, and age specific estimates, additive effect of age, multiplicative effect of year
		.	Constant
4	ρ	Best ₁	Best structure from Step 1 ($\rho_{\text{Site} \times \text{Survey effort} + \text{Age class}}$)
	ϕ	Best ₂	Best structure from Step 2 ($\phi_{\text{Year} + \text{Age class} + \text{HY}(\text{Banding} + \text{Hatch})}$)
	ψ	Best ₃	Best structure from Step 3 ($\psi_{\text{Site} + \text{Age class}}$)
		Best ₃ + Habitat _{emigration}	Best structure from Step 3, additive effect of habitat area on emigration
		Best ₃ + Habitat _{immigration}	Best structure from Step 3, additive effect of habitat area on immigration
		Best ₃ + Habitat _{emigration} + Habitat _{immigration}	Best structure from Step 3, additive effects of habitat area on emigration and immigration
		Best ₃ + Age class \times Habitat _{emigration}	Best structure from Step 3, additive effect of age-specific emigration based on habitat area
		Best ₃ + Age class \times Habitat _{immigration}	Best structure from Step 3, additive effect of age-specific immigration based on habitat area
		Best ₃ + Age class \times (Habitat _{emigration} + Habitat _{immigration})	Best structure from Step 3, additive effect of age-specific emigration and immigration based on habitat area

Appendix C. Model ranking results for a multi-state mark-recapture model of transition (ψ), survival (ϕ), and detection (p) rates of adult (>1 year post-hatch) and hatch-year (“HY”; 1 year post-hatch) piping plovers on the Niobrara River, NE and the Lewis and Clark Lake and Gavins Point Reach segments of the Missouri River, NE/SD (2011–2016).

Step ^a	ψ^b	ϕ^c	p^d	k^e	$\Delta QAIC_c^f$	Weight	Deviance
4	Age class + Site + Age class \times Habitat _{Emigration}	Age class + Year + HY(Banding + Hatch)	Age class + Site \times Survey effort	24	0.00	0.34	5102.91
4	Age class + Site + Habitat _{Emigration} + Habitat _{Immigration}	Age class + Year + HY(Banding + Hatch)	Age class + Site \times Survey effort	24	0.58	0.25	5103.49
4	Age class + Site + Habitat _{Emigration}	Age class + Year + HY(Banding + Hatch)	Age class + Site \times Survey effort	23	0.71	0.24	5105.66
4	Age class + Site + Age class \times (Habitat _{Emigration} + Habitat _{Immigration})	Age class + Year + HY(Banding + Hatch)	Age class + Site \times Survey effort	26	1.86	0.13	5100.70
4	Age class + Site + Age class \times Habitat _{Immigration}	Age class + Year + HY(Banding + Hatch)	Age class + Site \times Survey effort	24	5.71	0.02	5108.62
3	Age class + Site	Age class + Year + HY(Banding + Hatch)	Age class + Site \times Survey effort	22	6.77	0.01	5113.75
4	Age class + Site + Habitat _{Immigration}	Age class + Year + HY(Banding + Hatch)	Age class + Site \times Survey effort	23	8.07	0.01	5113.01
3	Age class + Site + Year	Age class + Year + HY(Banding + Hatch)	Age class + Site \times Survey effort	27	12.07	0.00	5108.87
2	Age class + Site \times Year	Age class + Year + HY(Banding + Hatch)	Age class + Site \times Survey effort	46	15.98	0.00	5073.79
1	Age class + Site \times Year	Age class + Site + Year + HY(Banding + Hatch)	Age class + Site \times Survey effort	48	17.54	0.00	5071.21

3	Site	Age class + Year + HY(Banding + Hatch)	Age class + Site × Survey effort	21	27.70	0.00	5136.71
3	Site + Year	Age class + Year + HY(Banding + Hatch)	Age class + Site × Survey effort	26	33.78	0.00	5132.62
2	Age class + Site × Year	Age class + HY(Banding + Hatch)	Age class + Site × Survey effort	42	34.11	0.00	5100.17
2	Age class + Site × Year	Age class + Site + HY(Banding + Hatch)	Age class + Site × Survey effort	44	34.74	0.00	5096.68
3	Site × Year	Age class + Year + HY(Banding + Hatch)	Age class + Site × Survey effort	45	46.88	0.00	5106.75
1	Age class + Site × Year	Age class + Site + Year + HY(Banding + Hatch)	Site × Survey effort	47	51.08	0.00	5106.82
1	Age class + Site × Year	Age class + Site + Year + HY(Banding + Hatch)	Age class + Site + Survey effort	46	79.97	0.00	5137.78
1	Age class + Site × Year	Age class + Site + Year + HY(Banding + Hatch)	Site + Survey effort	45	94.56	0.00	5154.43
3	Age class + Year	Age class + Year + HY(Banding + Hatch)	Age class + Site × Survey effort	21	127.89	0.00	5236.89
1	Age class + Site × Year	Age class + Site + Year + HY(Banding + Hatch)	Site	44	128.85	0.00	5190.79
3	Year	Age class + Year + HY(Banding + Hatch)	Age class + Site × Survey effort	20	139.40	0.00	5250.44
3	Age class	Age class + Year + HY(Banding + Hatch)	Age class + Site × Survey effort	17	143.95	0.00	5261.07

1	Age class + Site × Year	Age class + Site + Year + HY(Banding + Hatch)	Age class + Site	45	151.46	0.00	5211.33
3	.	Age class + Year + HY(Banding + Hatch)	Age class + Site × Survey effort	16	151.51	0.00	5270.65

^a We undertook modeling in four successive steps to reduce the total number of models under consideration. We developed the best general models for p , ϕ , and ψ (steps 1–3, respectively) to which we added specific ecological hypotheses about movement (step 4).

^b Transition rate was predicted to vary by: Age class – hatch-year (“HY”; 1 year post-hatch) or adult (>1 year post-hatch), Habitat_{Emigration} – the area of potential nesting habitat at a site affects the emigration rate from that site, Habitat_{Immigration} – the area of potential nesting habitat at a site affects the immigration rate to that site, Site – Gavins Point Reach, Lewis and Clark Lake, or Niobrara River, and Year – 2011–2016.

^c Survival rate was predicted to vary by: Age class – hatch-year (HY; 1 year post-hatch) or adult (>1 year post-hatch), Year – 2011–2016, Banding – age in days at banding (affected hatch-year birds only), Hatch – hatch date standardized to 20 April = 0 (affected hatch-year birds only), and Site – Niobrara River, Gavins Point Reach, or Lewis and Clark Lake.

^d Detection probability was predicted to vary by: Age class – hatch-year (HY; 1 year post-hatch) or adult (>1 year post-hatch), Site – Niobrara River, Gavins Point Reach, or Lewis and Clark Lake, and Survey effort – binary variable representing different monitoring intensity depending on level of bird activity and project focus (pre-2015 or post-2015).

^e Number of parameter in the model.

^f Akaike’s Information Criterion corrected for small sample size and overdispersion ($\hat{c} = 1.07$). Minimum QAIC_c = 5151.26.

CHAPTER II: HABITAT SELECTION AND NEST SUCCESS OF PIPING PLOVERS AND LEAST TERNS ON THE NIOBRARA RIVER, NEBRASKA

Abstract

Guiding effective species conservation often involves identification of habitats where animals can successfully reproduce. In response to observed local population declines, we studied nest-site selection and nest success of two imperiled species, the piping plover (“plover”, *Charadrius melodus*) and interior least tern (“tern”, *Sternula antillarum athalassos*), breeding on the Niobrara River, Nebraska, 2010–2016. Our objectives were to identify habitat characteristics of nest sites and determine if those same habitat characteristics were predictive of nest success. We compared 155 used (63 plover and 92 tern nests) vs. 292 randomly chosen unused locations, and 73 successful (hatched ≥ 1 egg) vs. 79 unsuccessful nests. Plovers and terns selected nest sites that were farther than unused sites from the vegetated riverbank ($\beta = 1.793$, 95% CI = 1.348–2.238), which was the closest potential source of avian and mammalian predators. To a lesser degree, birds selected sites surrounded by dry sand ($\beta = -1.517$, 95% CI = -1.953–-1.081), but showed no preference for distance to water. Despite selecting nest sites that appeared primarily to minimize predation risk, flooding was the main cause of nest failure. The habitat variables that we measured were not related to nest success, which could be due to birds selecting nest sites based on unmeasured habitat characteristics or to promote reproductive success at other stages of life history (e.g., chick or adult survival), but also may indicate a mismatch between the environmental cues birds are using to select nesting habitat and the suitability of that habitat. Anthropogenic impacts to this relatively natural river from upstream effects of mainstem Missouri River dams and climate change related increases in precipitation and storms may be making Niobrara River sandbar habitat more prone to flooding and less suitable to successful plover and tern nesting.

Introduction

Population declines have been recorded in North American breeding shorebirds (Andres et al. 2012), and although multiple factors contributed to these declines, habitat change likely is an important driver (Thomas et al. 2006). Habitat choices occur at each stage of a bird’s annual cycle (Rosenzweig 1985, Skagen and Knopf 1994, Gill et al. 2001), but selective pressure for suitable breeding habitat may be especially strong because habitat must sustain eggs, nestlings, and attending adults (Ibáñez-Álamo et al. 2015). Nest-site selection can influence adult survival (Amat and Masero 2004, Miller et al. 2007), nest success (Stokes and Boersma 1998, Murray and Best 2014), and survival of young (Blomqvist and Johansson 1995, Gibson et al. 2016), and ultimately, habitat preferences are expected to correlate with fitness (Orlans and Wittenberger

1991, Clark and Shutler 1999). The relationship between nest-site selection and reproductive success is widely studied (Cody 1985, Jones 2001), yet frequent incongruences between selection and success illustrate the complexity of the relationship (Chalfoun and Schmidt 2012). Despite this mismatch, knowledge of nest-site selection can have important implications for guiding conservation, particularly for rare species and sensitive habitats, as species recovery often depends on protection and management of suitable habitat (Mayor et al. 2009).

Prairie rivers of the Great Plains, USA, provide important breeding habitat for the federally threatened and endangered piping plover (“plover”, *Charadrius melodus*) and interior least tern (“tern”, *Sternula antillarum athalassos*; USFWS 1985a, b). The species nest sympatrically on open to sparsely vegetated areas of river sandbars in sand and fine gravel substrates (Schwalbach 1988, Kirsch 1996) and have similar nesting habitat preferences (Maslo et al. 2016). Population declines in plovers and terns are attributed in part to change or loss of riverine sandbar breeding and brood-rearing habitat (USFWS 2009). Monitoring, research, and management of populations nesting on heavily modified rivers (e.g., the Missouri River; Catlin et al. 2015) have demonstrated an important role of habitat in regulating plover and tern populations (Catlin et al. 2011b, Anteau et al. 2014b). Anthropogenic alteration of river flow for flood control, irrigation, hydropower, and other purposes, can reduce quantity and quality of sandbar habitat by inhibiting sediment deposition, allowing for vegetation encroachment (Benjankar et al. 2012) and establishment (Currier 1982), and intensifying sandbar erosion (Schmidt and Graf 1990, Hazel et al. 2010). The Niobrara River in northern Nebraska is considered one of the last minimally regulated rivers in the Great Plains (Ethridge et al. 1999, Galat et al. 2011) that supports breeding plovers and terns (Ferland and Haig 2002, USFWS 2009, PRRIP 2015). The small number of engineered structures and streamflow diversions (Alexander et al. 2009) contributes to a relatively uninterrupted flow, and the Niobrara has been proposed as a model natural river system for guiding water management strategies amenable to plover and tern nesting (Adolf et al. 2001). However, despite its natural setting, plover and tern use of the Niobrara River has decreased in the last 10 years.

Because habitat affects plover and tern populations (Hunt et al. 2018), understanding nest-site selection could provide clues to population changes on the Niobrara River. Plovers and terns can exhibit high nest-site fidelity between years (Atwood and Massey 1988, Friedrich et al. 2014), but in a dynamic river system, shifting sandbar availability may prohibit birds from selecting nest sites based on experience or knowledge. Instead, they may need to assess nest sites yearly, based on habitat features that cue protection from sources of nest failure, among other things. Previous research indicates that plovers and terns select nest-sites away from dense vegetation and water, which may minimize the risk of nest depredation (Espie et al. 1996, Shaffer et al. 2013) and nest flooding (Burger 1987, Espie et al. 1996), respectively. For coastal and riverine-nesting birds, nest-site selection may reflect a balance of the risks of

predation and flooding to nest success (Storey et al. 1988, Greenberg et al. 2006, DeRose-Wilson et al. 2013). Our objectives in this study were to 1) identify habitat characteristics selected by plovers and terns, and 2) assess whether nest-site habitat was related to nest success. Given that predation and inundation are the main sources of nest failure in associated systems (Kirsch 1996, Catlin et al. 2011b), we expected that nest-site selection would reflect predator and inundation avoidance, and successful nests would be those that maximized habitat characteristics related to protection from depredation and flooding. Specifically, we hypothesized that nests would be located in patches of dry sand and away from water to reduce the risk of flooding, and nests would be away from the riverbank, where tall and or dense vegetation provides the nearest potential source of predator habitat. We predicted that there would be congruence between the preferred habitat variables and nest success (hatching ≥ 1 egg).

Methods

Study Area

We studied plovers and terns on 65 river km of the Niobrara River in northeastern Nebraska between the Spencer Hydropower plant (42°48'N, 98°39'W), a hydroelectric facility through which water runs freely, to the confluence of the Niobrara and Missouri Rivers (42°45'N, 98°03'W; Figure 1). This stretch of the Niobrara River is characterized by a wide valley and broadly braided, sand-bed channel, with clusters of emergent sandbars (Johnsgard 2007, Alexander et al. 2010). River flow is driven by groundwater, with an increasing influence of flashier, precipitation-runoff hydrology (Alexander et al. 2009). The downriver half of the study area is part of the Missouri National Recreational River. Adjacent land cover is a mix of marsh floodplain, wooded riparian corridor, wetlands, natural floodplain and upland forest communities, pastureland, and croplands.

Field Methods

We surveyed open to sparsely vegetated areas of emergent sandbars from April–August, 2010–2016, in search of plover and tern nests. Nests consist of a small, shallow scrape (8–9 cm wide, 1–2 cm deep) in sand that may be lined with a thin layer of pebbles. We located nests by grid-searching potential nesting habitat, using spotting scopes to look for incubating birds, and recognizing behavioral cues of adult birds (e.g., territorial and distraction displays). Upon discovery, we logged each nest location with a handheld GPS unit (Trimble Geo XT, Trimble Navigation, Ltd., Sunnyvale, CA). Geographic coordinates had a horizontal accuracy of ± 15 cm.

We floated the eggs to estimate developmental stage (Westerskov 1950) and calculate the expected hatch date (plovers – 34 days from nest initiation; Elliott-Smith and Haig 2004, terns – 24 days from nest initiation; Thompson et al. 1997). We attempted to check each nest

every 2–7 days throughout the incubation period to determine nest fate, increasing our visit frequency within 3 days of the estimated hatch date when possible. If we observed ≥ 1 chicks or if ≥ 1 eggs disappeared within 2 days of the estimated hatch date without material evidence of failure (e.g., eggs washed out of nest bowl, predator tracks at nest, bloody egg shell), we considered a nest successful (Catlin et al. 2015, Hunt et al. 2018). When no obvious signs of failure were present, but eggs disappeared > 2 days before estimated hatch date, we considered the nest failed due to unknown cause. Common causes of plover and tern nest failure are depredation, flooding, weather-related events such as heavy rain or hail, sandbar erosion, and abandonment. Potential nest predators in this region included raccoons (*Procyon lotor*), coyotes (*Canis latrans*), American crows (*Corvus brachyrhynchos*), and American mink (*Neovison vison*). Placement of wire predator exclosures (Melvin et al. 1992) around plover nests is a common management practice to increase nest success (Johnson and Oring 2002, Tan et al. 2015), but none of the nests in this study were exclosed.

Land cover classification

To describe habitat characteristics of plover and tern nests, we developed land cover data for the study area using four-band digital imagery from the USDA Farm Service Agency's National Agricultural Imagery Program (NAIP). NAIP imagery has ≤ 1 m resolution and a horizontal accuracy of ± 6 m (U.S. Department of Agriculture 2016). Although we surveyed for nests 2010–2016, NAIP imagery was not collected in 2011, 2013, or 2015, so we developed land cover datasets for 2010, 2012, 2014, and 2016. We classified land cover using object-oriented methods in the program eCognition Essentials 1.3 (Trimble 2016). Object-oriented classification is beneficial when pixel size is small relative to the objects of interest (Blaschke 2010). The two-step classification process entailed 1) multiresolution segmentation, in which adjacent pixels sharing common spectral characteristics were grouped into objects based on user-defined size, shape, and texture parameters, and 2) a supervised classification of the objects. We determined through an exploratory visual inspection that suitable parameters for segmentation of our imagery were a size scale of 4, a shape smoothness/compactness ratio of 0.4/0.6, and a color/shape ratio of 0.9/0.1. We trained the classification in 3 delineated regions of interest, each approximately 100 ha, that represented a variety of land cover types. We assigned segments in each region of interest to a land cover class based on familiarity with the study area and ground-validation data collected in 2016. We used the k-nearest neighbor classifier algorithm ($k = 3$) to implement the classification on the entire scene. We aggregated the classification output to a minimum feature size of 10 m².

Our primary focus of the classification was the identification of 4 habitat types of ecological relevance to plovers: dry sand (nesting habitat), wet sand (foraging habitat), water, and vegetation. To distinguish the statistical signatures of these habitat types and to improve classification accuracy, we classified the imagery into 15 land cover classes and then grouped

the 15 classes into the 4 habitat types (Appendix A). We summarized the area of each habitat type in each year to investigate trends in land cover change.

Nest and random point attributes

We extracted habitat data related to each plover and tern nest from the classified land cover datasets. We calculated the shortest distance from each nest to water to assess potential flood avoidance. We calculated the shortest distance from each nest to the vegetated channel boundary (hereafter, “bank”) to assess potential predator avoidance. Although some sandbars had patches of dense vegetation, the patches were small (typically <1 ha) and did not have mature trees that could serve as raptor perches, so we considered them unlikely to support mammalian or avian predators that nesting plovers or terns would avoid. To characterize the habitat surrounding nests, we calculated the amount of each habitat type (dry sand, wet sand, water, vegetation) within 46 m of each nest location (Figure 2). The area within a 46 m radius circle centered on a nest (hereafter, “nest area”) represents a hypothetical piping plover nesting territory of 0.67 ha, based on an average nesting density of approximately 1.5 pairs/ha in a nearby population (Catlin et al. 2015).

We collected the same habitat data for approximately twice the number of random points as nests, per year, for nest-site selection models. We constrained random points to habitat types amenable to plover and tern nesting (see Appendix A). To avoid repeated sampling of the same area, we spaced each random point at least 92 m from the next nearest nest or random point (so that the nest areas would not overlap). We used ArcGIS 10.5 (ESRI, Redlands, CA, USA) to generate random points and to derive habitat data from the classified imagery.

Statistical analyses

Preliminary analyses. We conducted two preliminary analyses to maximize the number of observations per parameter in our logistic regression models for nest-site selection and nest success. First, we reduced the number of independent variables under consideration and controlled for multicollinearity using a principal components analysis (PCA) on the four habitat types within a nest or random area. PCA converts a set of possibly correlated variables into a reduced set of linearly uncorrelated variables with maximum variance, and it can improve estimation of logistic model parameters (Aguilera et al. 2006). We included the first component in each analysis and any subsequent components necessary to bring the cumulative variation explained to $\geq 75\%$.

Second, we evaluated differences in habitat characteristics of plover and tern nests to determine if we could pool data for the two species, thereby increasing the number of observations per model covariate and reducing bias on regression coefficients (Peduzzi et al. 1996). Though plovers and terns have different foraging strategies and nesting densities (Baasch et al. 2017), which might influence nest-site selection, in general, the species use

similar habitats (Maslo et al. 2016). We used an information theoretic approach to compare logistic mixed effects models (1 = plover nest, 0 = tern nest), with year as a random effect to account for potential temporal dependence (Crawley 2012). Specifically, we compared a null model (intercept only) to a global model containing our habitat variables: distance to water, distance to bank, and the first two principal components representing land cover within a nest area. We considered nest-site selection, based on the habitat variables that we measured, to be similar between plovers and terns if the null model outcompeted the global model.

Nest-site selection analysis. We investigated the effects of distance to bank, distance to water, and surrounding land cover on nest-site selection by comparing these variables at actual nests to unused random points using logistic regression (Hosmer et al. 2013). We modelled nest-site selection using logistic mixed effects models (1 = actual nest, 0 = random point) with a random effect for year. Because of frequent surveys and conspicuous behavior of nesting adults on small islands, we assumed that the response variable was recorded without error. We developed ten candidate models representing biologically relevant hypotheses and used an information theoretic approach to select the model that best fit the data.

Nest success analysis. To examine the role of habitat selection on reproductive success, we compared habitat characteristics of successful and failed nests using logistic mixed effects models (1 = successful nest, 0 = failed nest), with a random effect for year. We used the same set of 10 candidate models and the same information theoretic approach to model selection as in the nest-site selection analysis so that we could examine the relationship between nest-site selection and nest success.

Model selection. For our information theoretic approach, we calculated Akaike's Information Criterion corrected for small sample size (AIC_c) for each model and compared models by the difference in AIC_c value (ΔAIC_c) from the model with the lowest AIC_c value and by Akaike weight (w_i ; Burnham and Anderson 2002, Wagenmakers and Farrell 2004). Additionally, we calculated conditional (fixed effects only) and marginal (fixed effects and random effect) pseudo- R^2 values (Nakagawa and Schielzeth 2013) to better understand model fit and variation (Symonds and Moussalli 2011). We considered covariate effects meaningful if 95% confidence intervals of β coefficients did not include 0 and if presence of a covariate improved the model fit, compared to a similar model without that covariate (Arnold 2010). For beta estimates, we provided estimates from the top-ranked model (Cade 2015).

For each analysis, we standardized all linear covariates (mean = 0.0, SD = 1.0) to aid in model fitting and interpretation, and we carried out a separate PCA to capture the variation specific to each dataset. We assessed collinearity among the principal components and other variables using Pearson's correlation coefficient (r) and variance inflation factors (VIFs). We performed all analyses in the R statistical program version 3.4.0 (R Development Core Team 2017). We fit logistic mixed effects models with package "lme4" (Bates et al. 2014), performed

model selection and averaging using package “MuMIn” (Bartón 2012), and conducted PCA using package “stats”. Means are reported as mean \pm 1SD.

Results

We found 155 nests (63 plover, 92 tern) during the breeding seasons of 2010, 2012, and 2016, and visited nests every 6.4 ± 3 days. There were no nests in 2014. We assessed the fate of 152 nests: 73 were successful (18 plover, 29%; 55 tern, 60%) and 79 failed (42 plover, 37 tern). Nests failed primarily to flooding (35%), unknown cause (35%), and predation (11%). Nests that failed for unknown cause were likely depredated, because material signs of flooding were easy to detect (e.g., overwashed sandbar, eggs floating in nest cup or washed downstream of the nest cup), and predator tracks and sign can be masked by wind and rain. Nest success rates were similar in 2012 and 2016 (61% and 64%, respectively), and lowest in 2010 (30%), when approximately half of all nests failed due to flooding or flood-related sandbar erosion.

The number of nests in a given year was correlated positively with the total amount of dry sand ($r = 0.70$) and negatively with the amount of wet sand ($r = -0.89$) within 46 m of the nest (Figure 3), though with only 4 sample points, these trends should be interpreted cautiously. Nest success rate was not correlated with amount of land cover type (Figure 3). Across years, the amount of dry sand (335 ± 106 ha) and wet sand (251 ± 61 ha) were the most variable, while water (930 ± 25 ha) and vegetation (447 ± 59 ha) area varied less (Figure 3).

Land cover composition surrounding nests and random points was explained by the first two principal components (PC1 and PC2, respectively), which comprised $\geq 75\%$ of the cumulative variation in each dataset. Therefore, we included these two variables in all model sets. PC1, PC2, distance to bank, and distance to water were not highly correlated (all $r < 0.7$, all VIFs < 3) and thus were used in the same models simultaneously (Zuur et al. 2010, Hosmer et al. 2013).

Plovers and terns did not appear to select habitat differently from one another. The null model for species-specific nest-site selection, which included only an intercept term and a random effect for year, was the best supported model ($w_i = 0.88$; $\Delta AIC_c = 3.99$ to next model). Moreover, the global model explained very little variation in species-specific nest-site selection (marginal pseudo- $R^2 = 0.09$), collectively indicating that nest site selection did not differ greatly between plovers and terns relative to the variables we measured (Table 1). Thus, we proceeded by modeling nest site selection and nest success using pooled data for the two species.

Nest-site selection

Overall nest-site selection was influenced by all measured habitat variables (marginal pseudo- $R^2 = 0.82$; Table 2), but based on effect size, nests were most clearly distinguished from random points by their distance to the riverbank ($\beta = 1.793$, 95% CI = 1.348 –2.238; Table). Nests were nearly twice as far from the bank as random points, on average, and every nest was >60 m from the bank (Table). Surrounding land cover also was a strong predictor of nest-site

selection. The first principal component described land cover based on a dryness gradient that differentiated dry sand from wet sand and water (Appendix B, Appendix). Both nest areas and random areas were dominated by dry sand, but the proportion of dry sand was significantly greater in nest areas than in random areas (PC1, $\beta = -1.517$, 95% CI = $-1.953 - -1.081$; Table 4). The second principal component further described land cover in nest and random areas based on the amount of vegetation or wet sand (Appendix B, Appendix). The presence of PC2 in the top-ranked model provided some indication that plovers and terns selected for wet sand and avoided vegetation, but confidence intervals for the estimate overlapped 0 (Table 3). Distance to water also was included in the top model, and nest locations tended to be farther from water compared to random locations, but there was substantial variation surrounding mean values (Table 4), and the effect was relatively weak with confidence intervals that included 0 (Table 3). Additionally, the second-ranked model, which excluded only distance to water, was highly competitive with the top model ($\Delta AIC_c = 0.58$, $w_i = 0.38$; Table 2) and provided a plausible explanation for nest-site selection.

Nest success

Although there were clear patterns of non-random nest placement for both species, we did not detect habitat selection differences between successful and failed nests. Mean variable values did not differ between successful and failed nests (Table 4) and there was considerable uncertainty in selecting a model that best explained nest success, as nine models had $\Delta AIC_c < 4$ (Table 5). Our best supported model was the null model, which contained only an intercept term and random effect for year (Table 5). The global model had a marginal pseudo- R^2 of 0.18, indicating a reasonable fit to the data (Møller and Jennions 2002, Symonds and Moussalli 2011).

Discussion

River sandbar habitat is dynamic and can change substantially from year to year, affecting the wildlife populations that depend on it. On the lower Niobrara River, the amount of plover and tern nesting habitat decreased over the duration of our study, and the number of nests was correlated with the amount of nesting habitat. Inundation and predation were the main sources of nest failure, and plover and tern nest-site selection indicated some degree of protection from flooding and predation. However, the habitat characteristics that plovers and terns selected were unrelated to nest success, and in fact, nest success was not predicted by any of the habitat variables we measured.

Nest site selection

Plover and tern nest-site selection on the lower Niobrara River was most strongly influenced by distance to riverbank, supporting our expectation that plovers and terns would avoid predator habitat and perches. In our study area, the riverbank was marsh floodplain,

forest, and pasture and croplands, and was the nearest potential source of avian and mammalian predators. Plover and tern nest sites were on average ~150 m from the bank, which is similar to both the maximum probability of use distance between plover nests and predator perches in central Nebraska (Baasch et al. 2017), and the distance at which tree removal “made it more difficult for avian predators to observe plover nests and chicks” in prairie Canada (Maxson and Haws 2000). Plover and tern breeding abundance and habitat selection on the Missouri River also is positively related to distance from predator perches (Shaffer et al. 2013, Anteau et al. 2014a), and in general, avoidance of potential predator perches and habitat edges is exhibited across shorebird species (MacDonald and Bolton 2008). Reduced peak and annual flows allows vegetation to encroach on sandbars connected to the river bank, effectively shrinking the river channel (Williams 1978). The increased amount of dense vegetation that we observed in 2014 may have narrowed the channel and limited the ability of plovers and terns to select nest sites that were a suitable distance from the bank, contributing to the absence of nesting in that year.

Beyond maximizing distance from potential raptor perches, avoidance of the riverbank also could indicate a preference for mid-channel sandbars. Mid-channel bars are surrounded by water on all sides and occur in areas where the river is naturally wider. They may provide the best isolation from mammalian predators, assuming that animals would not swim to a mid-channel bar as readily as they would walk onto a shoreline-attached bar. Even though narrower river reaches were found to have the highest proportion of potential plover and tern nesting habitat (unvegetated to lightly vegetated dry sand) on the Lower Platte and Missouri rivers (Elliott and Jacobson 2006), nesting plovers and terns across the Great Plains preferentially use wider reaches. On the Missouri River, there was a small positive effect of channel width on the number of plover and tern pairs (Shaffer et al. 2013), and on the Central and Lower Platte rivers, plovers and terns tend to nest on sites with a wide active channel and large mid-channel sandbars (Ziewitz et al. 1992, Kirsch 1996). A meta-analysis of Nebraska rivers found the probability of plover and tern nesting colony incidence increased with increasing channel width (PRRIP 2015). If the benefit of using mid-channel sandbars is protection from mammalian predators, plovers and terns that select these sites may trade-off the threat of mammalian predation with other risks. Plovers in North Dakota nested more densely on islands than on bank-attached sandbars (Anteau et al. 2014a), however, due in part to the prevalence of avian, rather than mammalian predators, mid-channel and shoreline nests had similar daily survival rates (Anteau et al. 2012a). Wide channel areas also are flat and may not create island sandbars high enough in elevation to protect nests from flooding (Ziewitz et al. 1992).

In addition to selecting nest sites away from the riverbank, we found that plovers and terns used nest sites surrounded by predominantly dry sand, with little wet sand or water nearby. Dry sand is less sensitive to water level fluctuations than wet sand (Elliott 2011), and

therefore assumed to be high in elevation relative to the water level. Fine-scale elevation data were not available in this study, so we inferred selection for dry sand as selection for high elevation areas of sandbars. On the Missouri River, tern preference for dry sand compared to silt nesting substrate was associated with higher elevation bars (Stucker et al. 2013). Use of dry sand habitat also is consistent with observations of plovers and terns nesting at locations higher in elevation relative to the water line than availability would indicate at off-channel habitat of the Platte River (Baasch et al. 2017). The advantage of nesting in dry sand substrate presumably is protection from nest flooding, which provides some support for our hypothesis that plovers and terns would select nest sites protected from inundation.

We expected that plovers and terns would further reduce the risk of nest inundation during periods of high river flow by selecting nest sites away from the river channel, however, we found that nests were no farther from water than random points. The average nest in our study was 44 m from water, which is similar to observations of plover and tern nests along the Central Platte River (55 m and 89 m, respectively; Baasch et al. 2017) and plover nests on the lakeshore habitat in Saskatchewan (54 m; Espie et al. 1996). Plovers preferentially forage along waterlines, where prey abundance is high relative to dry and vegetated habitats (Le Fer et al. 2008), and chicks reared in these high-quality habitats experience growth and survival benefits (Catlin et al. 2014). Plover broods that hatched from nests >50 m from the shoreline have been documented shifting to areas closer to or on the shoreline (Wiltermuth et al. 2015). The pattern of plover nest sites located approximately 50 m from water across multiple Great Plains systems suggests that the distance may represent a balance that optimizes the benefits of proximity to high-quality foraging habitat and protection from inundation. Though we detected no differences in nest-site selection between plovers and terns, studies incorporating elevation data show that terns tend to nest farther from water and at higher elevations than plovers (Faanes 1983, Baasch et al. 2017), presumably because they are not constrained to defend and use foraging areas near their nests. Terns may feed within 100 m of nests (Faanes 1983), but they also will readily travel to foraging locations 1.5 km to >10 km away (Wilson et al. 1993, Sherfy et al. 2012), and so are not expected to base local-scale nest selection on food resources.

On coastal habitat in particular, plover and tern nest-site selection is seen as a balance between distance to water (high-tide line) and distance to vegetation (dunes), due to the linear nature of the habitat (Burger 1987, Patterson et al. 1991). The slight positive correlation ($r = 0.16$) between nest distance to vegetation and distance to water in our study, however, indicates that nests farther from the bank also tended to be farther from water, suggesting use of larger, mid-channel sandbars. The channel width of the Niobrara (88–329 m within ~5 km of the mouth; Ethridge et al. 1999) limits sandbar width, and thus constrains the distance that nests on mid-channel bars can possibly be from water. For example, in 2016, island bars that

supported plover and tern nests were approximately 100 m wide on average, so naturally, many nests could not be more than 50 m from the channel.

Nest success

Predation often is the primary cause of nest failure in plovers (Cohen et al. 2009, Catlin et al. 2011b) and is an important factor in tern reproductive success (Kirsch 1996, Brooks et al. 2013). Despite a demonstrated preference for nest sites away from predator habitat and perches in this study and across the Great Plains breeding range, we did not find that distance to the bank affected nest success as we predicted. In our study, predation accounted for only 11% of the known nest failures, although it could have been the cause of many unidentified nest failures (35% of failed nests). Predation pressure on plover and tern nests can vary widely among sites, but in the Great Plains typically nest predators are mammalian rather than avian (Mayer and Ryan 1991, Kruse 1993, Ivan and Murphy 2005). If avian predators are more common than mammalian predators at a site, then avoidance of the riverbank may have little effect on nest success, and instead benefit nesting birds in other aspects of life history, like adult or chick survival. In the northern Great Plains, adult plover depredation by raptors correlated with the amount of tree cover within 2 km and was not detected in sites where trees were scarce (Murphy et al. 2003). Adult mortality often results in nest abandonment (Roche et al. 2010), and the low rate of abandonment that we observed (6% of failed nests), coupled with an adult survival rate consistent with neighboring populations (Chapter I of this thesis, Hunt et al. 2018), suggests that plovers and terns successfully selected nest sites that minimized adult mortality. Chick survival decreased with proximity of nests to trees in the Great Lakes (Brudney et al. 2013), and avian predation was a known source of chick mortality on riverine and lake habitat in the Great Plains (Kruse 1993, Ivan and Murphy 2005, Catlin et al. 2011a). Plover chick survival on the Niobrara was comparable with observations from other populations, but it depended largely on river flow (Chapter I of this thesis).

Plovers and terns selected nest sites predominantly based on distance to predator habitat, yet flooding was at least as great a cause, if not the primary cause, of nest failure. Nesting birds preferred dry sand sites, which we expected would protect nests from flooding, however, dry sand sites provided no reproductive advantage. It is possible that the amount of dry sand surrounding the nest site was not an accurate indicator of sandbar elevation above the water, and therefore would not protect nests from inundation. We also expected that nests away from water would be more likely to hatch, but distance to water did not predict nest success. Flooding on the Niobrara was at times catastrophic, with entire sandbars submerged during periods of high river flow. When this degree of flooding occurred during plover and tern nesting, it is possible that nests were inundated regardless of their distance to the river channel.

More plover nests than tern nests flooded (43% vs. 27% of nest failures, respectively), despite being located in similar habitats. Overall plover nest success rate (29%) on the Niobrara was within the range of observations elsewhere (3–84%; see Table 1 in Catlin et al. 2015), and lower than the mean rate for nests not protected with predator cages or fencing (approximate mean: 47%; see Figure 2 in Anteau et al. 2012a). Overall tern nest success (60%) was within the range of observations from other sites (40–94%; Kruse et al. 2001, Szell and Woodrey 2003, Elliott et al. 2007, Jenniges and Plettner 2008). The lower overall nest success rate in plovers compared to terns is partially attributable to annual variation. During the 2010 nesting season, exceptionally high water flow lead to extensive flooding that similarly affected plover and tern nest success. In subsequent years, water flow was not as high, and nest flooding was not as widespread. Compared to terns, relatively few plovers used the Niobrara 2012–2016 when nest flooding was less common, which accounts for some of the difference in overall species-specific nest success rates. Flood and storm-caused nest failure is related to farther and more frequent dispersal in plovers (Haig and Oring 1988, Roche et al. 2012). Plovers on the Niobrara may have dispersed in response to widespread nest flooding in 2010, particularly to abundant habitat on the Missouri River (Chapter I of this thesis). Different life history strategies, such as longer incubation period, which naturally exposes eggs to threats over a longer period, and different nest defense and incubation behaviors (Smith et al. 2007) may also account for differences in species-specific nest success rates.

Similar to other studies, we were able to identify patterns of nest site selection based on habitat characteristics, but not nest success (Murphy et al. 1997, Chase 2002, MacDonald et al. 2016, McFarland et al. 2017). Ground-nesting shorebirds must consider a range of habitat features for nest placement that minimize predation and inundation and optimize conditions for incubation and chick rearing. Plovers and terns on the Niobrara River exhibited patterns of nest site selection that were consistent with other populations, including showing relatively stronger avoidance of depredation compared to flooding, and locating nests roughly 150 m from predator habitat and 50 m from water, providing evidence that those were the conditions under which the species adapted nest-site preferences. In other systems where inundation was a major threat to nest success, nests that were farther from water were less likely to flood (Espie et al. 1996) and the relative elevation of plover nests above the water level had a strong positive relationship with daily survival rate (Anteau et al. 2012a). In human-modified landscapes, novel environmental conditions can lead to mismatches between nest-site selection and nest success in plover and tern populations, including on barrier island beaches (Burger 1984, 1987), reservoirs (Anteau et al. 2012b), and on moderately to highly regulated rivers (Zeigler et al. 2017, Farnsworth et al. 2017). The lack of relationship between selection and success suggests that birds currently may be exhibiting non-ideal habitat selection in the face of changing environmental conditions, by selecting sites primarily for protection from

predators though they face potentially high risk of flooding. Conversely, because the habitat characteristics of successful and failed nests were highly similar, it is possible that birds may be selecting the best available habitat, but nest success is not related to habitat characteristics. This could be the case if nest success was dependent on an abiotic factor, such as extreme temperature (Farrell et al. 2018), or if high water events were intense enough that nests were equally susceptible to inundation regardless of their location.

Conservation Implications

Plovers and terns nesting on highly modified river and reservoir habitat have faced widespread flooding when water levels were manipulated (Anteau et al. 2012a). The Niobrara River has few impoundments and a relatively unregulated flow, but conditions for nesting plovers and terns may be declining due to indirect impacts of human activities, including upstream effects of mainstem Missouri River dams and climate related changes. Since construction of mainstream dams on the Missouri River, the Niobrara River has transitioned from a system with deep, stable channel and large sandbars to increasingly braided and shallow (Skelly et al. 2003), as Missouri River dams have reduced that river's capability to clear sediment from the mouth of the Niobrara (Ethridge et al. 1999, Bristow et al. 1999). Concurrent with the shift towards shallower habitat, there is a long-term upward trend in streamflow in the Niobrara watershed (Norton et al. 2014) and an increase in the frequency and intensity of extreme precipitation events in the central U.S. (Kunkel et al. 2012). These changes may pose increasing threats of flooding to nesting plovers and terns.

Flooding of nests and chicks is a natural event on unregulated rivers (e.g., (Sidle et al. 1992)), but the outsized effect of flooding on nest success, the selection for nesting habitat based more strongly on predator avoidance than flood avoidance, and the lack of protection afforded by dry sand nest sites that we observed could indicate that plovers and terns on the Niobrara face levels of flooding for which they are not adapted. Understanding the nature of habitat selection and reproductive success relationships is especially important for habitat specialists, because they are particularly vulnerable to changing conditions and are often species of conservation concern. For sandbar habitat on the Niobrara to be selected by plovers and terns, it should have large patches of dry sand located away from the riverbank. If sandbar habitat on the Niobrara River is to be amenable to plover and tern nest success, it must provide protection from over-wash by floods. Identifying and promoting the processes that contribute to creation and maintenance of high-elevation sandbars on the Niobrara is an important next step towards effective management of nesting plovers and terns.

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Tables

Table 1. Model ranking results for a random effects logistic regression model of species-specific nest site characteristics of piping plover and least tern nest sites on the Niobrara River, NE (2010–2016).

Model^a	k^b	ΔAIC_c^c	w_i	R_c^2^d	R_m^2^e
Year	2	0.00	0.88	0.00	0.05
Year + Distance to Bank + Distance to Water + PC1 + PC2	6	3.99	0.12	0.05	0.09

^a Predictors for nest site characteristics of piping plovers and least terns included: Distance to Bank – nearest distance from a nest location to the riverbank, Distance to Water – nearest distance from a nest location to water, PC1 – the first principal component describing land cover composition within a nest site (0.67 ha surrounding the nest location), PC2 – the second principal component describing land cover composition within a nest site, Year – a random effect of annual variation. All linear covariates were standardized (mean = 0.0, SD = 1.0). All models include an intercept.

^b Number of parameters in the model.

^c Akaike’s Information Criterion corrected for small sample size. Minimum $AIC_c = 209.77$.

^d Conditional pseudo- R^2 .

^e Marginal pseudo- R^2 .

Table 2. Model ranking results for a random effects logistic regression model of piping plover and least tern nest site characteristics on the Niobrara River, NE (2010–2016).

Model^a	k^b	ΔAIC_c^c	w_i	$R_c^2^d$	$R_m^2^e$
Year + Distance to Bank + Distance to Water + PC1 + PC2	6	0.00	0.51	0.80	0.82
Year + Distance to Bank + PC1 + PC2	5	0.58	0.38	0.79	0.81
Year + Distance to Bank + Distance to Water + PC1	5	2.93	0.12	0.74	0.77
Year + Distance to Water + PC1 + PC2	5	88.70	0.00	0.79	0.80
Year + Distance to Bank	3	90.45	0.00	0.77	0.77
Year + PC1 + PC2	4	91.60	0.00	0.54	0.55
Year + Distance to Water + PC1	4	112.17	0.00	0.58	0.60
Year + PC1	3	119.53	0.00	0.53	0.55
Year + Distance to Water + PC2	4	265.85	0.00	0.13	0.13
Year	2	290.72	0.00	0.00	0.00

^a Predictors for nest site characteristics included: Distance to Bank – nearest distance from a nest or random location to the riverbank, Distance to Water – nearest distance from a nest or random location to water, PC1 – the first principal component describing land cover composition within a nest or random site (0.67 ha surrounding the nest or random location), PC2 – the second principal component describing land cover composition within a nest or random site, Year – a random effect of annual variation. All linear covariates were standardized (mean = 0.0, SD = 1.0). All models include an intercept.

^b Number of parameters in the model.

^c Akaike’s Information Criterion corrected for small sample size. Minimum $AIC_c = 290.31$.

^d Conditional pseudo- R^2 .

^e Marginal pseudo- R^2 .

Table 3. Beta estimates and 95% confidence intervals for the effect of variables on piping plovers and least terns nest-site selection on the Niobrara River, NE (2010–2016). Estimates are from the top-ranked random effects logistic regression model.

Variable^a	Estimate	Lower 95% CI	Upper 95% CI
Intercept	-1.983	-2.855	-1.111
Distance to Bank	1.793	1.348	2.238
Distance to Water	-0.473	-1.062	0.116
PC1	-1.517	-1.953	-1.081
PC2	-0.970	-1.973	0.033

^a Predictors for nest site (1) vs. random site (0) characteristics included: Distance to Bank – nearest distance from a nest or random location to the riverbank, Distance to Water – nearest distance from a nest or random location to water, PC1 – the first principal component describing land cover composition within a nest or random site (0.67 ha surrounding the nest or random location), PC2 – the second principal component describing land cover composition within a nest or random site, Year – a random effect of annual variation. All linear covariates were standardized (mean = 0.0, SD = 1.0).

Table 4. Comparisons (mean \pm 1SD, range) of habitat variables at successful (hatched \geq 1 egg) and failed nest sites, and random sites, for piping plovers and least terns nesting on sandbars along the Niobrara River, NE (2010–2016).

Habitat Variable	Nest site (N = 155)	Random site (N = 292)	Successful nest (N = 73)	Failed nest (N = 79)
Distance to Bank (m)	169.4 \pm 34.5 (64–236)	87.9 \pm 57.4 (1–274)	171.8 \pm 34.7 (74–236)	167.3 \pm 35.1 (64–231)
Distance to Water (m)	44.1 \pm 27.9 (0–115)	31.3 \pm 51.5 (0–454)	42.9 \pm 26.6 (0–115)	44.8 \pm 29.5 (2–109)
Percent Dry Sand	84.3 \pm 20.5 (4–100)	43.5 \pm 30.3 (0–100)	84.2 \pm 21.1 (12–100)	84.0 \pm 20.3 (4–100)
Percent Wet Sand	5.4 \pm 10.7 (0–69)	21.6 \pm 19.8 (0–97)	6.3 \pm 11.0 (0–69)	4.8 \pm 10.7 (0–67)
Percent Vegetation	0.1 \pm 0.6 (0–8)	11.0 \pm 17.6 (0–86)	0.0 \pm 0.3 (0–2)	0.1 \pm 0.9 (0–8)
Percent Water	10.2 \pm 14.9 (0–68)	23.9 \pm 21.5 (0–88)	9.5 \pm 13.5 (0–59)	11.1 \pm 16.3 (0–68)

Table 5. Model ranking results for a random effects logistic regression model of piping plover and least tern nest success on the Niobrara River, NE (2010–2016).

Model^a	k^b	ΔAIC_c^c	w_i	$R_c^2^d$	$R_m^2^e$
Year	2	0.00	0.25	0.00	0.09
Year + PC1	3	0.83	0.17	0.01	0.12
Year + Distance to Bank	3	0.97	0.16	0.01	0.10
Year + Distance to Water + PC2	4	1.91	0.10	0.02	0.16
Year + Distance to Bank + Distance to Water + PC1	4	1.98	0.09	0.02	0.13
Year + Distance to Water + PC1	4	2.25	0.08	0.02	0.15
Year + PC1 + PC2	4	2.81	0.06	0.01	0.12
Year + Distance to Bank + PC1 + PC2	5	3.99	0.03	0.02	0.13
Year + Distance to Water + PC1 + PC2	5	4.00	0.03	0.02	0.16
Year + Distance to Bank + Distance to Water + PC1 + PC2	6	4.83	0.02	0.04	0.18

^a Predictors for nest success included: Distance to Bank – nearest distance from a nest location to the riverbank, Distance to Water – nearest distance from the nest location to water, PC1 – the first principal component describing land cover composition within a nest site (0.67 ha surrounding the nest location), PC2 – the second principal component describing land cover composition within a nest site, Year – a random effect of annual variation. All linear covariates were standardized (mean = 0.0, SD = 1.0). All models include an intercept.

^b Number of parameters in the model.

^c Akaike’s Information Criterion corrected for small sample size. Minimum $AIC_c = 206.44$.

^d Conditional pseudo- R^2 .

^e Marginal pseudo- R^2 .

Figures

Figure 1. Map showing the extent of the lower Niobrara River study area in northeast Nebraska (65 river km), USA from the Spencer hydropower plant to the HW-12 bridge in Niobrara, NE near the Niobrara-Missouri River confluence, where we located and monitored piping plover and least tern nests on river sandbars (2010–2016).

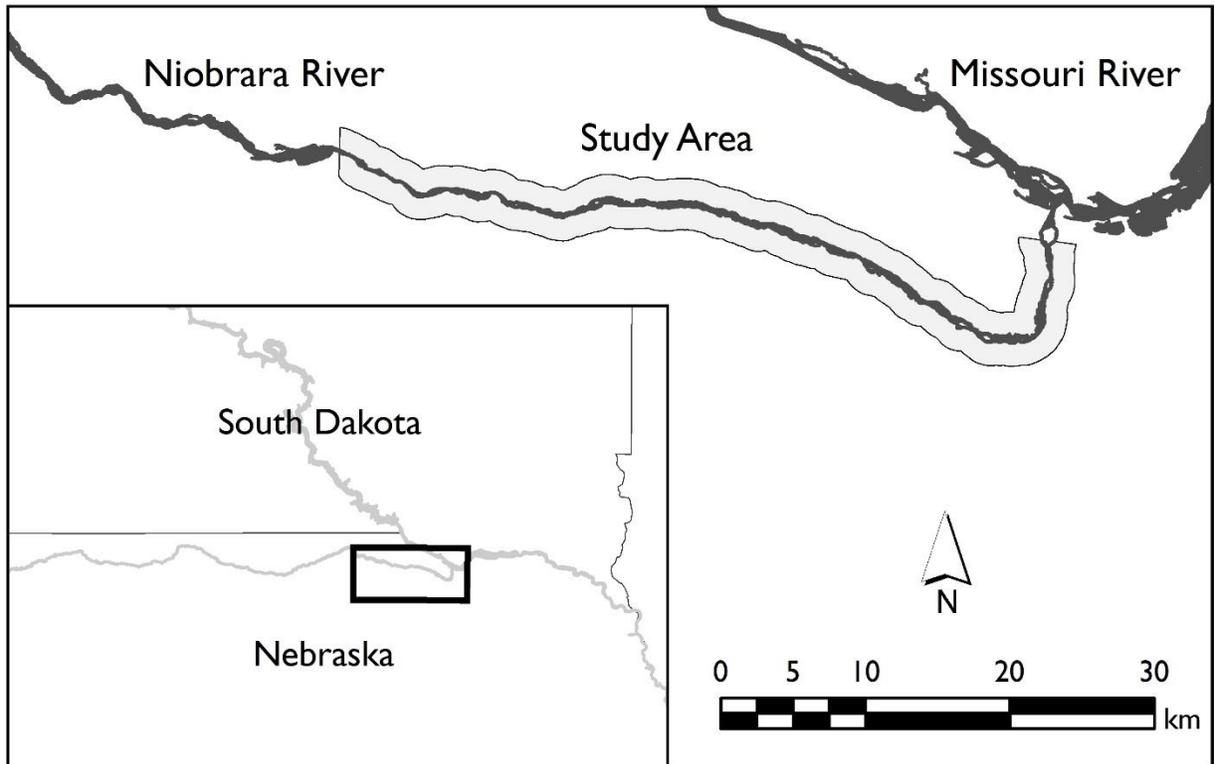


Figure 2. Example of raw (A) and classified (B) imagery of a portion of our study area on the Niobrara River, NE. We measured the distance from each nest location (triangle) to water and vegetation along the river bank, and quantified the amount of each habitat class (Nesting habitat = open to sparsely vegetated dry and damp sand, Forging habitat = open to sparsely vegetated wet sand, Vegetation, Water) in the 46 m surrounding the nest (circle), which represents an approximate territory size of 0.67 ha.

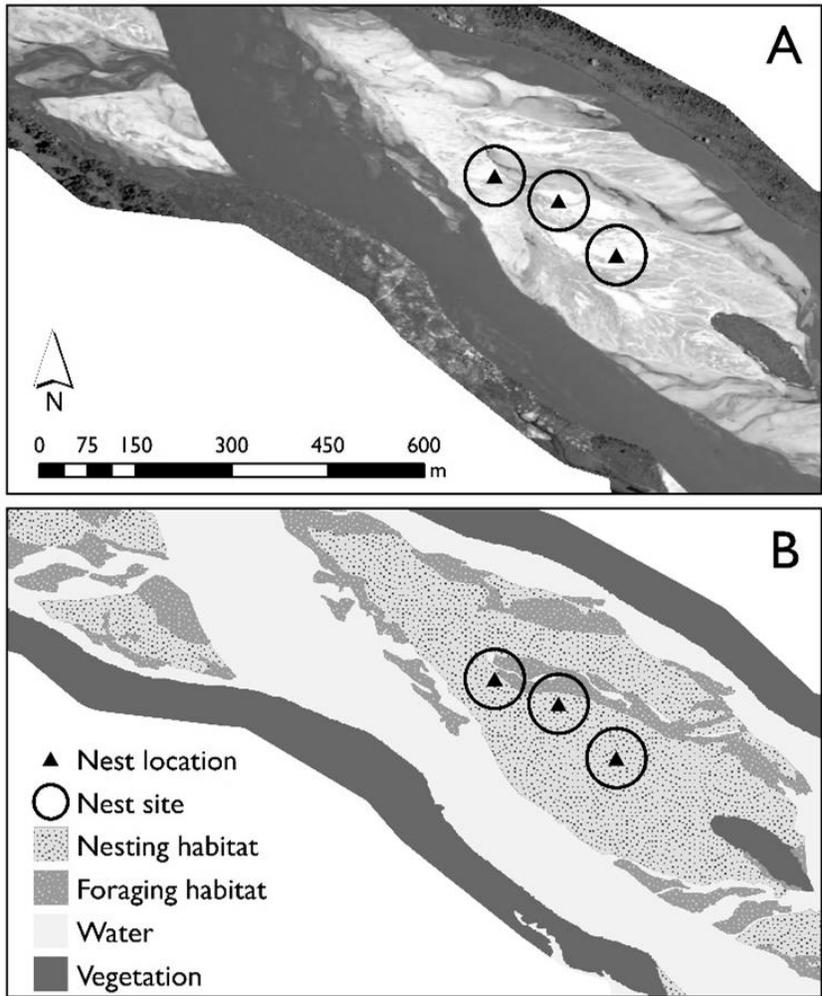
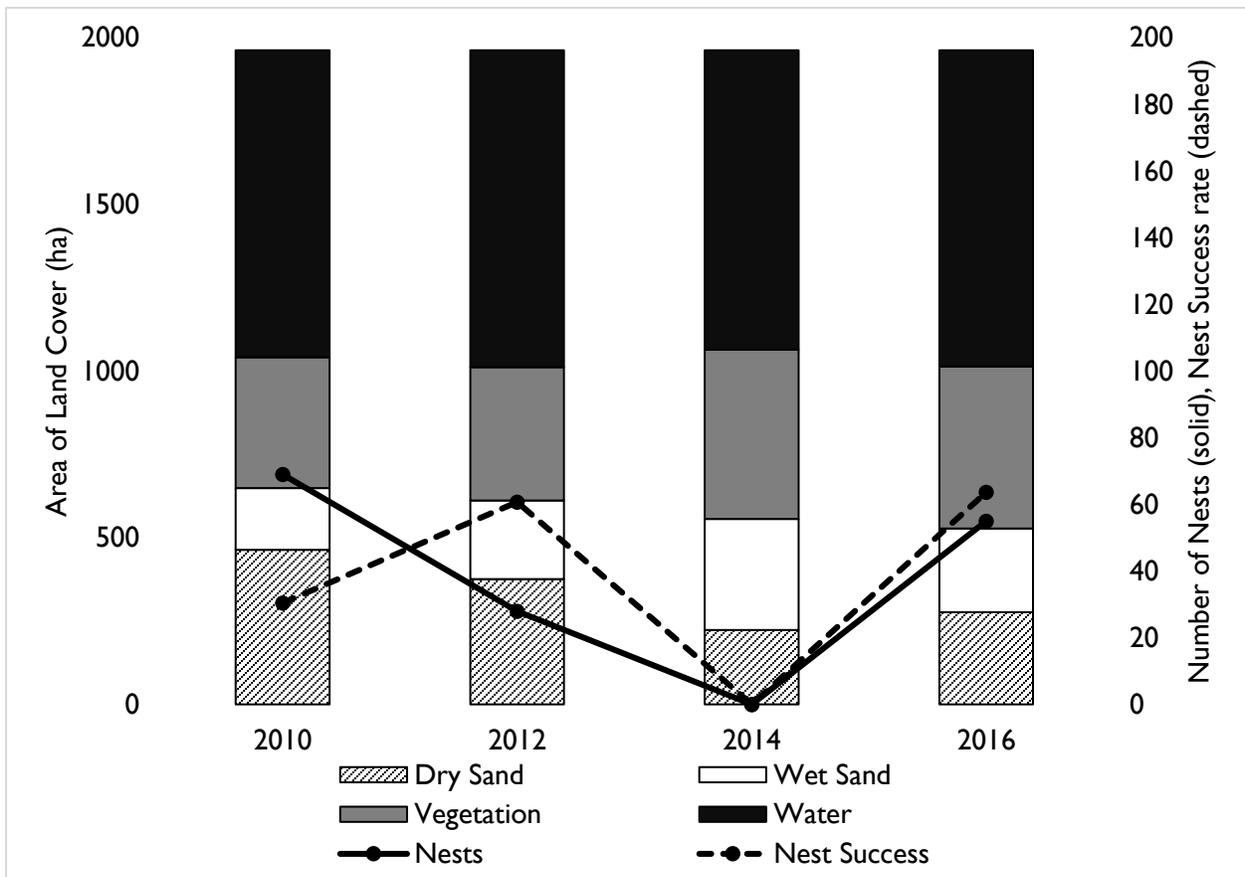


Figure 3. Area of land cover on the Niobrara River, NE, from Spencer hydropower plant to the HW-12 bridge in Niobrara, NE near the Niobrara-Missouri River confluence (65 river km), 2010–2016. Dry sand includes open to sparsely vegetated (<30% ground cover) dry to damp substrate, Wet Sand includes open to sparsely vegetated (<30% ground cover) wet sand and silt substrate, Vegetation is any area with dense (>30% ground cover) vegetation, and Water includes the river and areas of standing water. The solid line indicates the number of piping plover and tern nests in each year, and the dashed line indicates the nest success rate (percent of nests in which ≥ 1 egg hatched).



Supplemental Material

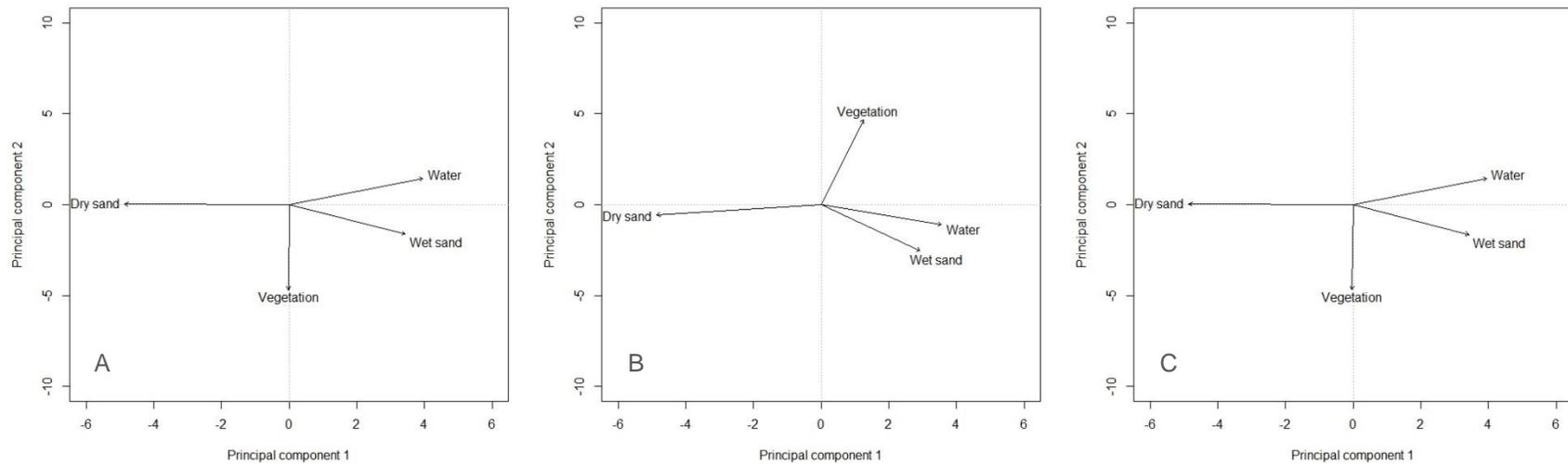
Appendix A. Land cover types and associated piping plover and least tern habitat classes identified in a supervised, object-oriented classification of imagery of the Niobrara River, NE. High-resolution digital imagery was obtained from the USDA Farm Service Agency's National Agricultural Imagery Program for the years 2010, 2012, 2014, and 2016.

Habitat type	Land cover class	Description
Nesting habitat	Dry sand	Unvegetated dry sand substrate
	Damp sand	Unvegetated damp sand substrate
	Dry sand, sparse vegetation	Dry sand with <30% ground cover
	Damp sand, sparse vegetation	Damp sand with <30% ground cover
Foraging habitat	Wet sand	Unvegetated wet sand substrate
	Muddy sand	Unvegetated deposition of silt
	Wet sand, sparse vegetation	Wet sand with <30% vegetation
	Muddy sand, sparse vegetation	Muddy sand with <30% vegetation
Water	Shallow water	Water with sand visible beneath the surface
	Deep water	Water with no sand visible beneath the surface
Vegetation	Vegetation	Dense ($\geq 30\%$) vegetation, including grasses, forbs, sedges, and other herbaceous riparian vegetation, and willow (<i>Salix spp.</i>), cottonwood (<i>Populus spp.</i>), and other riparian woody shrubs and trees
	Agricultural fields	Planted and fallow fields and rangeland

Appendix B. Factor loadings for principal components analysis of land cover surrounding piping plover and least tern nest locations and random locations on the Niobrara River, NE 2010–2016. In each dataset, the first two principal components explained $\geq 75\%$ of the cumulative variation.

Dataset	N	Variable	PC1	PC2
Species-specific nest-site selection	155	Dry Sand	-0.665	0.004
		Wet Sand	0.496	-0.234
		Water	0.559	0.204
		Vegetation	-0.005	-0.951
Nest-site selection	447	Dry Sand	-0.685	-0.087
		Wet Sand	0.469	-0.384
		Water	0.513	0.150
		Vegetation	0.218	0.907
Nest success	152	Dry Sand	-0.665	0.005
		Wet Sand	0.495	-0.238
		Water	0.559	0.206
		Vegetation	-0.006	-0.949

Appendix C. Plots of the first and second principal components describing land cover surrounding piping plover and least tern nest locations and random locations on the Niobrara River, NE 2010–2016. We did a separate principal components analysis for each dataset that we analyzed: species-specific nest-site selection (“A”; $N = 155$), nest-site selection (“B”; $N = 447$), and nest success (“C”; $N = 152$). In each dataset, the first two principal components explained $\geq 75\%$ of the cumulative variation.



CHAPTER III: CONCLUSIONS

Piping plover conservation and management in the Great Plains has focused largely on regulated systems, including those with flow diversions (e.g., Platte River), impoundments, reservoirs, and controlled river flow (e.g., Missouri River). However, the recent (2010–2016) plover population decline on the Niobrara River, a system with few diversions and impoundments, has brought attention to the state of breeding plovers in a relatively “natural” area. Previous research demonstrated the important roles of habitat and river flow in regulating plover populations (Sidle et al. 1992, Catlin et al. 2011, 2013; Anteau et al. 2014, Buenau et al. 2014, Hunt et al. 2018), and this study examines how these factors affect plover demography on the Niobrara River. The overall objective of this study was to understand piping plover demography and habitat availability on the Niobrara River, and understand how the Niobrara population is connected to the regional population. Here, I summarize the main results of my work and their relevance to piping plover conservation and management.

Summary of findings

Piping plover demography (2010–2016):

1. Daily nest survival on the Niobrara River was 0.995 ± 0.009 ($N = 115$), and the probability that a nest would survive from initiation to hatching was 0.21 (95% CI: 0.11–0.38). Nearly half of all nest failures on the Niobrara resulted from inundation, and flow increases 1 SD above the average daily maximum flow reduced the probability of nest success by more than half.
2. Chick survival rate from hatch to fledging on the Niobrara River was 0.54 ± 0.01 ($N = 66$) and was highest at low river flow. Direct flood-related chick mortality is difficult to document, but disappearance of pre-fledge chicks from recently over-washed sandbars provided strong evidence for its occurrence.
3. Across the regional population (Niobrara River, Lewis and Clark Lake segment of the Missouri River, Gavins Point Reach segment of the Missouri River), apparent survival of adults (≥ 1 year post-hatch) was greater than hatch-years (fledging age to one year post-hatch), and survival increased with year in both age classes (Adult: 0.68 ± 0.03 – 0.84 ± 0.03 ; HY: 0.16 ± 0.02 – 0.35 ± 0.06).
4. Breeding dispersal occurred throughout the regional population, but in successive years, plovers were significantly and substantially more likely to leave the Niobrara for Lewis and Clark Lake (0.51 ± 0.07) than to move between any other two sites. Overall, hatch-years were more likely to change sites (0.18 ± 0.03) than adults (0.09 ± 0.01), and hatch-year emigration increased when habitat availability was relatively low at the natal site, while adult emigration

increased when habitat availability was relatively high at their previous breeding site.

Piping plover habitat selection (2010, 2012, 2014, 2016):

1. Piping plovers ($N = 63$) and sympatric nesters, interior least terns ($N = 92$), selected nest sites with similar habitat characteristics, and their nest sites differed from random unused points ($N = 292$). Distance to the vegetated river bank had the strongest relative effect on selection, followed by the proportion of dry sand in the area surrounding a nest (0.67 ha circle centered on the nest, representing a hypothetical piping plover territory).
2. The habitat features associated with nest-site selection (farther to bank and greater amount of dry sand surrounding the nest) were not related to nest success (≥ 1 egg hatched). Successful nests ($N = 73$) and failed nests ($N = 79$) were not differentiated by the measured habitat characteristics.
3. On average, plover and tern nests were 169 ± 35 m from the riverbank, 44 ± 28 m from water, and were surrounded by 85% dry sand.

Conservation and Management Implications

An adequate balance of reproductive success, estimated in this study as nest and chick survival, and survival and return of hatch-year and adult birds is required to sustain a breeding population. Nest survival was within the range of values observed for the species (0.03–0.84; see Table 1 in Catlin et al. 2015), albeit on the low end, and was strongly negatively affected by increased water flow. Chick survival to fledging was higher than many other estimates from across the species range in some years (0.02–0.77; see Table 1 in Catlin et al. 2015), but also lower in some years, and declined sharply during increased river flow. Adult and hatch-year apparent survival rates were comparable to other populations (Adult: 0.51–0.81, HY: 0.29–0.53; see Table 2 in Catlin et al. 2015). Emigration rate from the Niobrara was higher than previously recorded in the regional population (0.00–0.32; see Figure 2 in Catlin et al. 2016), and many more birds left the Niobrara in successive years than entered it. Based on these data, the demographic rates that appear to have the greatest negative impact on population change on the Niobrara are lower nest survival and higher emigration than is generally observed in stationary or growing populations.

Nest survival on the Niobrara was largely determined by river flow. Plovers and terns on the Niobrara selected nest sites predominantly surrounded by dry sand habitat, indicating some degree of flood avoidance, given that dry sand is associated with sandbars that are relatively high in elevation above the water level (Stucker et al. 2013). Drier nest sites, however, afforded no reproductive advantage, as successful and failed nests were surrounded by nearly identical land cover. Nests were a similar distance to

water as in other populations (plovers = 55 m, terns = 89 m; Baasch et al. 2017), including where the distance decreased the risk of nest flooding (plovers = 54 m; Espie et al. 1996), but nests located farther from water were no more likely to hatch than those nearer water. If river flow is sufficient to over-wash entire sandbars, as was sometimes observed, then no distance to the river channel or amount of dry sand surrounding the nest site would protect a nest from flooding. Plovers may have selected dry sand nest sites approximately 50 m from the waterline as cues to high-quality nesting habitat, because these features are typically associated with elevated areas and prey-rich foraging areas (Le Fer et al. 2008).

Flooding is a natural event on unregulated rivers and has the potential to severely impact nest success (Sidle et al. 1992), but predation often is the primary cause of nest failure in plovers (Cohen et al. 2009, Catlin et al. 2011) and an important factor in tern reproductive success (Kirsch 1996, Brooks et al. 2013). For this reason, it follows that nest site selection was most strongly influenced by distance to the riverbank, i.e. the nearest potential source of avian and mammalian predators. Niobrara nest sites were a similar distance from predator habitat as nests in other Great Plains populations (150 m; Maxson and Haws 2000, Baasch et al. 2017). Nevertheless, nest success was not affected by the distance to predator habitat. Birds selected nest sites predominantly based on predator avoidance, yet flooding was at least as great a cause, if not the primary cause, of nest failure. The outsized effect of flooding on nest success, the lack of protection afforded by dry sand nest sites, and selection for nesting habitat based more strongly on predator avoidance than flood avoidance suggests that plovers and terns on the Niobrara face levels of breeding season flooding for which they are not adapted.

Plovers are territorial and loyalty to a breeding site is expected to confer advantages to fitness such as known foraging locations (Davies and Houston 1981) and predator communities (Yoder et al. 2004) as well as established relationships with neighbors (Krebs 1982). In this study, high probability of emigration from the Niobrara to Lewis and Clark Lake suggests that the benefits of changing sites outweighed the benefits of site fidelity. Plovers exhibit farther and more frequent dispersal following flood and storm-caused nest failure (Haig and Oring 1988, Roche et al. 2012), and the high rate of nest flooding on the Niobrara may have contributed to the high rate of emigration from that site.

Local population declines of species that occupy successional habitats are expected; as habitat develops and becomes unsuitable for the species in an area, individuals may move to areas of suitable habitat (Newton 1998). Accordingly, regional interchange among plover subpopulations occurs when habitat is higher-quality at one site compared to another (Catlin et al. 2016). Over the study, Niobrara sandbars

generally became more vegetated and saturated (decreased ratio of dry to wet sand), while on the Missouri, an abundance of high-quality nesting habitat was created by sustained flooding 2010–2011 (Catlin et al. 2015, Hunt et al. 2018). The high dispersal rate from the Niobrara to the Missouri River, especially the nearby Lewis and Clark Lake segment, likely reflects this difference in relative habitat quality. Likewise, during Missouri River flooding, habitat was completely submerged on the Gavins Point Reach and limited on Lewis and Clark Lake, and the Niobrara provided habitat for displaced Missouri River birds. The increased emigration rates of adult birds from sites with high amounts of nesting habitat relative to the average amount is likely an artifact of birds returning to Lewis and Clark Lake after temporarily shifting to the Niobrara during Missouri River flooding 2010–2011. We did not detect a significant temporal effect in dispersal probability, but newly created Missouri River habitat may have continued to draw birds from the Niobrara over the course of a few years, given that population density remained below carrying capacity until at least 2015 (Hunt et al. 2018).

The frequency of movements in response to shifting habitat quantity and quality between the Niobrara and the Missouri rivers, especially the Lewis and Clark Lake segment, highlights connection between these sites and the important role of the Niobrara in the regional plover population. During this study, birds moved from declining habitat on the Niobrara to new habitat on the Missouri. Nest and chick survival on Lewis and Clark Lake peaked within a few years of habitat creation (2014 and 2012, respectively), but have since steadily decreased. As Missouri River sandbars age, erosion and vegetation encroachment will reduce the quantity and quality of plover nesting habitat. Ensuring alternate habitat sources, like the Niobrara, could help sustain the regional population (Zeigler et al. 2017) as habitat on the Missouri River potentially becomes less suitable.

Although the Niobrara is considered one of the last minimally regulated rivers in the Great Plains (Ethridge et al. 1999, Galat et al. 2011), there are several indirect human impacts that pose a potential threat to plovers and their habitat. Mainstem dams on the Missouri River above and below the Niobrara-Missouri confluence modulate the Missouri River's flow and reduce its ability to clear sediment from the mouth of the Niobrara. This has resulted in formation of a sedimentary delta at the mouth of the Niobrara and has elevated water and sediment levels in the Niobrara (Ethridge et al. 1999, Bristow et al. 1999). Sediment deposition in the Niobrara River channel extends more than 22 km upriver from the mouth, and may lead to development of more bars rather than increase the size of pre-existing braid bars (Germanoski and Schumm 1993). Near the river mouth, the Niobrara has transitioned from a relatively deep, stable channel with large sandbars to become increasingly

braided and shallow (Skelly et al. 2003). This has effectively reduced the height of sandbars above the surface of the water, which may make them more susceptible to being inundated in periods of increased river flow.

Additionally, there is a long-term upward trend in streamflow in the Niobrara watershed (Norton et al. 2014) and an increase in the frequency and intensity of extreme precipitation events in the central U.S. (Kunkel et al. 2012). Intensification of storms may increase frequency and magnitude of flash flooding (Feng et al. 2016). There is an increasing influence of flashier, precipitation-runoff hydrology on the lower Niobrara (Alexander et al. 2009). During this study, periods of increased river flow during and following storms sometimes submerged entire sandbars or large swaths of breeding habitat. Extended periods of spring flooding build and maintain elevated, open sandbars, but short-duration, intense summer flows erode sandbar edges and redistribute sand from higher-elevation areas to lower-elevation areas (Hazel et al. 2010). These morphological and hydrological changes may negatively affect the suitability of Niobrara habitat by reducing height of sandbars above the channel and increasing the risk of inundation during surges in water flow.

For sandbar habitat on the Niobrara to be selected by plovers and terns, it should have large patches of dry sand located away from the riverbank. If sandbar habitat on the Niobrara River is to be amenable to plover and tern nest success, it must provide protection from over-wash by floods. Identifying and promoting the processes that contribute to creation and maintenance of high-elevation sandbars on the Niobrara is an important next step towards effective management of nesting birds

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