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RESEARCH ARTICLE

Demographic response of Piping Plovers suggests that engineered habitat restoration is no match for natural riverine processes

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ABSTRACT

Globally, riparian ecosystems are in decline due to anthropogenic modifications, including damming. Reduced frequency and altered timing of flood events decreases sandbar deposition, which reduces habitat for sandbar-breeding birds, including the threatened Piping Plover (*Charadrius melodus*). In response to limited breeding habitat and small populations, the U.S. Army Corps of Engineers constructed 255 ha of sandbar habitat on the Missouri River, USA, from 2004 to 2009. During the breeding seasons of 2010 and 2011, historically high flows resulted in the creation of 1,046 ha of suitable sandbar habitat on the Missouri River. We compared the demographic responses of Piping Plovers to this anthropogenic and natural habitat creation. We found that demographic parameters, including nest success ($\bar{x}_{\text{preflood}} = 0.45 \pm 0.02$ SE vs. $\bar{x}_{\text{postflood}} = 0.74 \pm 0.02$ SE), prefledging chick survival ($\bar{x}_{\text{preflood}} = 0.39 \pm 0.09$ SE vs. $\bar{x}_{\text{postflood}} = 0.65 \pm 0.03$ SE), and hatch-year survival ($\bar{x}_{\text{preflood}} = 0.16 \pm 0.03$ SE vs. $\bar{x}_{\text{postflood}} = 0.46 \pm 0.03$ SE), were consistently higher on the flood-created habitat than on the engineered habitat, leading to population growth after the flood. These differences were related to increased sandbar habitat, low nesting densities, and decreased nest and chick predation. As ecosystems are increasingly altered, ecologists seldom have the opportunity to make appropriate comparisons between managed and natural ecosystem processes. Our results suggest that management intervention may not be an appropriate substitute for natural ecosystem processes in riparian ecosystems.

Keywords: Charadrius melodus, Missouri River, flooding, habitat creation, riparian ecosystem, Piping Plover

La respuesta demográfica de *Charadrius melodus* sugiere que la restauración ingenieril del hábitat no es comparable con los procesos fluviales naturales

RESUMEN

A nivel global, los ecosistemas ribereños están disminuyendo debido a las modificaciones antropogénicas, incluyendo las represas. La reducción en la frecuencia y la alteración temporal de los eventos de inundación disminuyen el depósito de arena, lo que reduce el hábitat para las aves que anidan en los bancos de arena, incluyendo la especie amenazada *Charadrius melodus*. En respuesta a las condiciones de escasez del hábitat reproductivo y a las pequeñas poblaciones, el Cuerpo de Ingenieros del Ejército de EEUU construyó 255 ha de hábitat de bancos de arena en el Río Missouri entre 2004 y 2009. Durante las estaciones reproductivas de 2010 y 2011, los picos de inundación históricos generaron 1,046 ha de hábitat adecuado de bancos de arena en el Río Missouri. Comparamos la respuesta demográfica de *C. melodus* a las creaciones de hábitat antropogénico y natural. Encontramos que los parámetros demográficos, incluyendo el éxito del nido ($\bar{x}_{\text{pre-inundación}} = 0.45 \pm 0.02$ EE vs. $\bar{x}_{\text{post-inundación}} = 0.74 \pm 0.02$ EE), la supervivencia del polluelo antes del emplumamiento ($\bar{x}_{\text{pre- inundación}} = 0.39 \pm 0.09$ EE vs. $\bar{x}_{\text{post- inundación}} = 0.65 \pm 0.03$ EE) y la supervivencia al año de eclosión ($\bar{x}_{\text{pre- inundación}} = 0.16 \pm 0.03$ EE vs. $\bar{x}_{\text{post- inundación}} = 0.46 \pm 0.03$ EE), fueron consistentemente más elevadas en el hábitat creado por la inundación que en el hábitat construido, llevando a un aumento de la población luego de la inundación. Estas diferencias estuvieron relacionadas a un aumento en el hábitat de bancos de arena, bajas densidades de anidación y disminución en la depredación del nido y los polluelos. Debido a que los ecosistemas están cada vez más alterados, los ecologistas raramente tienen la oportunidad de realizar comparaciones apropiadas entre procesos ecosistémicos manejados y naturales. Nuestros resultados sugieren que la intervención de manejo puede no ser un sustituto adecuado para los procesos ecosistémicos naturales en los ecosistemas ribereños.

Palabras clave: Charadrius melodus, creación de hábitat, ecosistema ribereño, inundación, Río Missouri

INTRODUCTION

Humans have altered riparian ecosystems worldwide by constructing dams, channelizing rivers, and converting floodplains for agriculture or development. Two-thirds of ocean-bound fresh water is obstructed by more than 800,000 dams (Petts 1984, McCully 1996). Globally, more than 58% (172 of 292) of all large river systems have been regulated and fragmented by dams (Nilsson et al. 2005), including 85 of 139 systems in the Northern Hemisphere alone (Dynesius and Nilsson 1994, Nilsson and Berggren 2000). Riparian ecosystems provide habitats for many communities and species (Ward et al. 1999, Naiman et al. 2005), and are pathways for dispersal and migration (Naiman and Décamps 1997). Due to their complexity, riparian ecosystems are sensitive to variations in hydrology and often are early indicators of environmental change (Nilsson and Berggren 2000).

Numerous habitat changes have been linked to dams (Nilsson and Berggren 2000). Upstream terrestrial habitats are inundated and previously lotic (flowing water) habitats are converted to lentic (still water) habitats (Nilsson and Berggren 2000). Downstream, over-bank flooding is often reduced or shifted temporally, resulting in changes to the system's geomorphology, connectivity with the floodplain, forest communities, sediment cycling, and erosion rates (Nilsson and Berggren 2000). Moreover, dams can reduce sandbar deposition and river meandering (Johnson 1992). River regulation for human use especially affects plants and animals adapted to the natural dynamism of riparian ecosystems (Lytle and Poff 2004). Of 165 peer-reviewed papers examining flow alterations and ecological responses, 92% reported degraded values for recorded ecological metrics with only 13% reporting improvements (Poff and Zimmerman 2010).

The Missouri River in the USA is an example of a regulated river system. This river was historically dynamic, exhibiting 2 flow pulses per year that coincided with snow melt in the Great Plains, and in the mountains (Hesse and Mestl 1993, Galat and Lipkin 2000). Between 1937 and 1964 the U.S. Army Corps of Engineers (USACE) constructed 6 dams on the main stem of the river and channelized much of the lower Missouri River (U.S. Army Corps of Engineers 2006), which reduced flood frequency and suppressed within-year flood pulses (Hesse and Mestl 1993, Galat and Lipkin 2000), and ultimately resulted in a decrease of 96% of Missouri River sandbar habitat (Dixon et al. 2012). The current water management regime has resulted in fewer flood events and has led to a decrease in habitat for a suite of species including the Piping Plover (*Charadrius melodus*), Least Tern (*Sternula antillarum*), pallid sturgeon (*Scaphirhynchus albus*), and plains cottonwood (*Populus deltoides*; U.S. Fish and Wildlife Service 2003, Dixon et al. 2012, Johnson et al. 2015). In response, the USACE initiated ecosystem management specifically to recover these species and from 2004 to 2009 created 255 ha of emergent sandbar habitat for Piping Plovers and Least Terns (U.S. Fish and Wildlife Service 2000, 2003).

In 2010 and 2011, record high flows on the Missouri River inundated most sandbar habitat (U.S. Army Corps of Engineers 2012). In 2011, all available sandbar habitat below the Gavins Point Dam was inundated when flows from the Gavins Point Dam exceeded 2,831 $m^3\ s^{-1}$ for 85 days, with a maximum flow of 4,530 $m^3\ s^{-1}$ reached in July (U.S. Army Corps of Engineers 2012), as compared with the mean July flow from 2005 to 2009 of 748 $m^3\ s^{-1}$. The increased flows from the 2011 flood created a substantial amount of new sandbar habitat that could be utilized by Piping Plovers in subsequent breeding seasons. This rare flood event allowed us to compare the responses of Piping Plovers to anthropogenic vs. natural habitat creation.

We evaluated demographic responses (nest success, survival, fidelity, and population changes) of Piping Plovers between the large-scale management effort (sandbar habitat construction) and the results of the natural high-water event. From 2005 to 2009, research focused on evaluating demography and movement on new, 'engineered' sandbar habitat relative to 'natural' sandbar habitat that was deposited by high flows from 1996 to 1997 (Catlin 2009, Catlin et al. 2011b, 2015). From 2012 to 2014, we studied how Piping Plovers responded to the flood-created sandbar habitat.

METHODS

Study Species

The Piping Plover is an imperiled shorebird that breeds in 3 areas of North America—the Atlantic Coast from Newfoundland to North Carolina, the Great Lakes, and the Northern Great Plains from prairie Canada to Nebraska—and winters along the southeastern Atlantic Coast, the Gulf of Mexico, and the Caribbean. On the Missouri River, Piping Plovers nest on riverine sandbars on open, sparsely vegetated sand or gravel substrate with adjacent saturated or moist substrate for foraging and brood rearing (Elliott-Smith and Haig 2004, Catlin et al. 2015). In part due to a decrease in breeding habitat, Piping Plovers were placed on the U.S. Threatened and Endangered Species List in 1986 (U.S. Fish and Wildlife Service 1985, 2009).

Study Area

We studied Piping Plovers on the Gavins Point Reach of the Missouri River, which extends 95 km downriver from the Gavins Point Dam (42.8620°N, 97.4854°W; Figure 1), from 2005 to 2014 on 3 different sandbar types: (1) 'Preflood natural sandbars,' which were deposited during high flows from 1996 to 1997. These sandbars varied in

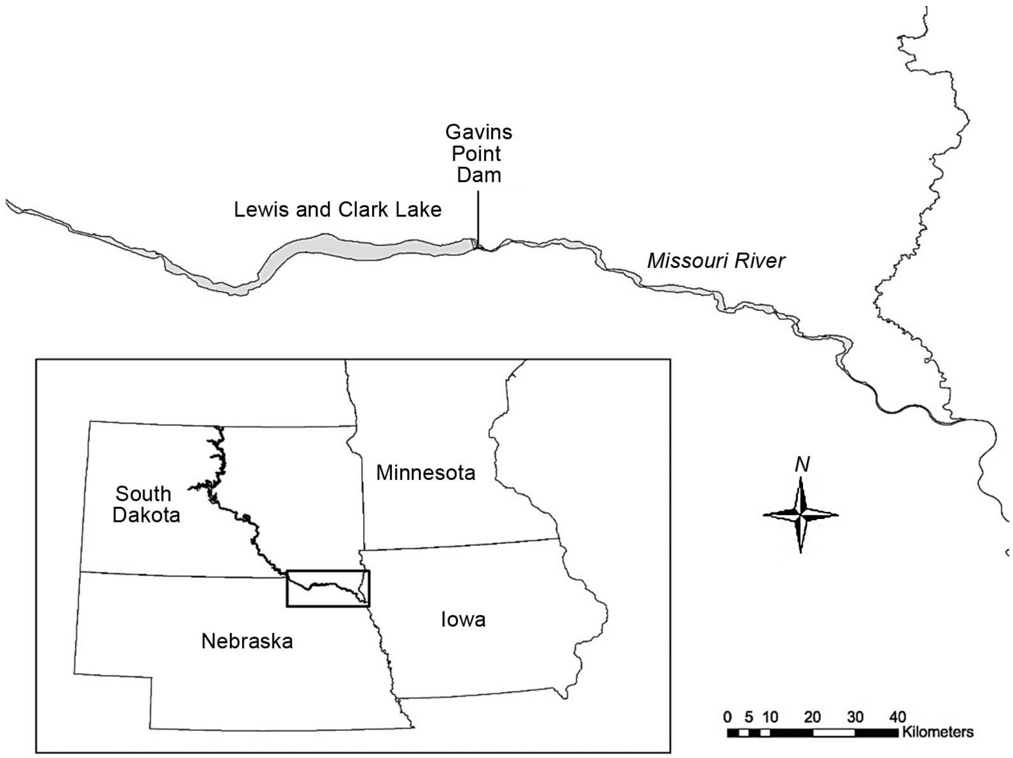

FIGURE 1. Map of the Missouri River, USA, showing the study location where we examined the demographic response of Piping Plovers (*Charadrius melodus*) to both anthropogenic and natural habitat creation on the Gavins Point Reach, downstream of the Gavins Point Dam, 2005–2014.

size and many were heavily vegetated during the preflood portion of our study (2005–2009; Catlin et al. 2015); (2) 'Preflood engineered sandbars,' which were created by the USACE from 2004 to 2009 by dredging sand from the river bottom, depositing the sand at the construction site, and leveling it with bulldozers (Figure 2A; Catlin et al. 2015). In general, engineered sandbars were constructed in locations where sandbars would naturally form and where historical Piping Plover nesting sandbars were located; and (3) 'Postflood natural sandbars,' which were created through sediment deposition during the 2011 flood (Figure 2B). The 2011 flood completely inundated all preflood sandbar habitat, such that there were no preflood sandbars (engineered or natural) present during the postflood period (2012–2014). Newly created sandbars (both engineered and flood created) consisted of high, barren sand nesting areas and low-lying, unvegetated sand and mudflats. As sandbars aged, they were colonized by cottonwoods (*Populus* spp.) and willows (*Salix* spp.). Common predators of shorebirds and their nests included American Crows (*Corvus brachyrhynchos*), Great Horned Owls (*Bubo virginianus*; Catlin et al. 2011a), American mink (*Neovison vison*), and northern raccoons (*Procyon lotor*; Catlin et al. 2011b).

Field Methods

Each breeding season (April–August), we searched sandbars for nests by walking transects through potential nesting habitat and observing Piping Plover behavior. We recorded nest locations using Trimble GPS units (Trimble Navigation, Sunnyvale, California, USA), and attempted to check nests every 2–3 days until failure or hatching. From 2005 to 2009, nest exclosures were used to protect 40–60% of nests from predators (Catlin et al. 2015). We captured adult Piping Plovers with drop-door or drop-box traps placed over nests, and uniquely marked captured individuals. We uniquely marked chicks as close to hatching as possible. We attempted to resight or recapture chicks every 2–4 days until they fledged ($\sim$25 days; Hunt et al. 2013) and continued to resight fledged chicks when possible. Throughout each breeding season, we used spotting scopes to resight previously banded Piping Plovers. We received supplementary color band resighting information for Piping Plovers from breeding, wintering, and migratory stopover locations outside our study area from cooperators.

Habitat Information

We calculated sandbar habitat availability using imagery collected during the 2005–2009 and 2012–2014 breeding

FIGURE 2. Examples of (**A**) preflood engineered sandbar habitat that was created by the U.S. Army Corps of Engineers (USACE; 2005–2009) by dredging sand from the river bottom, depositing it at the construction site, and leveling it with bulldozers (Catlin et al. 2015), and (**B**) postflood natural sandbar habitat that was created through sediment deposition during the 2011 flood on the Missouri River, USA. Photos provided by the USACE.

seasons. Pan-sharpened multispectral QuickBird (satellite) imagery (1 m resolution) was collected each year between April and October and classified using Definens Developer Software (L. Strong personal communication). We classified habitats into open and sparsely vegetated (<30% vegetative cover) or vegetated (>30% vegetative cover) dry or moist sand. The amount of suitable nesting habitat was calculated as the amount of open and sparsely vegetated wet and dry sand on a sandbar. We calculated the maximum number of active nests on each sandbar annually and estimated nesting density as pairs ha^{-1} for each sandbar.

Analytical Methods

Modeling approach. To test hypotheses related to the flood, we used models that explained the data in preflood conditions (Catlin et al. 2015) and then examined the effects on model fit of adding variables that described postflood conditions or the differences between preflood and postflood conditions. By so doing, we examined the effects of the flood while accounting for known variation in the preflood state (Table 1). In most cases, we tested for the effects of the flood by replacing year with the categorical variables preflood (2005–2009), flood (2010, 2011), and postflood (2012–2014; Table 1). In this study, we refer to 3 age-classes of Piping Plovers: adult or after-hatch-year (AHY; ≥1 yr posthatch), hatch-year (HY; from hatching to the following breeding season), and prefledging chicks (hatching to fledging; ~25 days posthatch). All survival analyses were performed in program MARK (White and Burnham 1999) using the R 3.2.0 (R Core Team 2015) package RMARK (Laake 2013). Unless otherwise stated, and to account for multiple competing models, we obtained model-averaged parameter estimates and unconditional standard errors for all real (e.g., survival, fidelity, detection rates) parameters (Burnham and Anderson 2002). For beta regression coefficients, we provide estimates from the top-ranked model (Cade 2015). When interpreting the difference between individual estimates, we used several types of evidence, including model ranking, the size of the estimate relative to the standard error, model weights, and confidence intervals. We interpreted differences based on these factors and in relation to other factors in our models and model sets. Results are presented as $\bar{x} \pm 1$ SE unless otherwise noted.

Nest success. We considered a nest successful if ≥1 egg hatched or if ≥1 egg disappeared without signs of predation or flooding within 2 days of the estimated hatching date. We used a random effects logistic exposure model (Rotella et al. 2000, Shaffer 2004, Stephens et al. 2004) to calculate the daily survival rate (DSR) of nests (Appendix B equation 3). We accounted for known variation from the preflood period (Table 1) and included a fixed effect for year and a random effect for sandbar in a given year to account for possible dependence among nests (Catlin et al. 2015). To calculate nest success, we exponentiated DSR estimates to 34, as 34 days is the common incubation period for Piping Plovers.

We hypothesized that nest success would be higher on postflood sandbars; however, we thought that nest success might decrease as the flood-created sandbar habitat aged (Table 2). To examine our hypotheses, we started with the global model from Catlin et al. (2015), with the addition of our density variable as nesting densities were substantially lower following the flood. We tested the goodness-of-fit of the global model (Hosmer and Lemeshow 1989). We used a stepped approach to modeling. In the first step, we removed variables that were not supported (Appendix A Table 4). We then tested for the effect of the flood. Finally, we added the age of the postflood sandbar habitat to the model containing the flood variable to examine changes in the effect of flooding over time. We used Akaike's information criterion corrected for small sample size (AIC_c; Burnham and Anderson 2002) to evaluate the effect of each step. If AIC_c increased after a step, we stopped the process and used the model with the lower AIC_c value.

Prefledging chick survival. We used a random effects Cormack-Jolly-Seber (CJS) model (Gimenez and Choquet 2010) to estimate age-specific daily survival (ϕ) and

TABLE 1. Descriptions, means, and standard errors of variables used in modeling nest success (NS), prefledging chick apparent survival ($\phi_{prefledging}$) and detection probability ($p_{prefledging}$), after-hatch-year (AHY) true survival (S_{AHY}) and fidelity (F_{AHY}), and hatch-year (HY) true survival (S_{HY}) and fidelity (F_{HY}) of Piping Plovers on the Gavins Point Reach of the Missouri River, USA, 2005–2014. Catlin et al. (2015) provided the basis for the expected relationships, as well as the justification for the addition of covariates to our demographic models.

Variable	Model	Description	NS	$\phi_{prefledging}$ and $p_{prefledging}$	S_{HY} and F_{HY}	S_{AHY} and F_{AHY}
Age	NS, $\phi_{prefledging}$, $p_{prefledging}$, S_{HY}, F_{HY}, S_{AHY}, F_{AHY}	For nest success, this refers to age (days) since nest initiation (standardized from April 20). For $\phi_{prefledging}$, this refers to the age of chicks in days since hatching. For AHY and HY true survival and fidelity, this refers to the difference in age classes (AHY vs. HY).	18.17 ± 0.09	—	—	—
Band age	S_{HY}, F_{HY}	The age (days since hatching) at banding (standardized from May 20).	—	—	1.80 ± 0.06	—
Clutch size	NS	The number of eggs in a clutch.	3.46 ± 0.01	—	—	—
Date	NS	The standardized date of nest observation (April 20 = 0).	54.16 ± 0.16	—	—	—
Density [a]	NS, $\phi_{prefledging}$, $p_{prefledging}$, S_{HY}, F_{HY}	Nest density: This refers to the sandbar and year-specific number of pairs ha^{-1}.	1.39 ± 0.01	1.16 ± 0.03	1.16 ± 0.03	—
Engineered	NS, $\phi_{prefledging}$, $p_{prefledging}$, S_{HY}, F_{HY}	Preflood engineered habitat: A categorical (1, 0) variable for engineered sandbar habitat (vs. natural habitat) created by the U.S. Army Corps of Engineers (USACE) during 2005–2009.	—	—	—	—
Engineered age	NS, $\phi_{prefledging}$, $p_{prefledging}$, S_{HY}, F_{HY}	Preflood engineered habitat age: The age (years since creation) of engineered habitat. This is a nested effect that only affects engineered habitat.	1.37 ± 0.01	1.30 ± 0.04	1.30 ± 0.04	—
Exclosure	NS	Nest exclosure: A categorical variable (1, 0) representing the presence or absence of a nest exclosure.	—	—	—	—
Flood	S_{AHY}, F_{AHY}	A categorical variable for the flood period (2010–2011). As there were no nests or chicks produced during this period, this was only applicable when modeling S_{AHY} and F_{AHY}.	—	—	—	—
Hatch	$\phi_{prefledging}$, S_{HY}	Hatching date: The standardized hatching date of prefledging chicks (May 20 = 0).	—	68.28 ± 0.30	68.28 ± 0.30	—
Postflood	NS, $\phi_{prefledging}$, S_{HY}, F_{HY}, S_{AHY}, F_{AHY}	A categorical variable for the postflood period (2012–2014).	—	—	—	—
Postflood age	NS	Postflood habitat age: The age (years since creation) of the postflood habitat. This is a nested effect that only affects postflood habitat.	1.40 ± 0.01	—	—	—
Preflood	NS, $\phi_{prefledging}$, S_{HY}, F_{HY}, S_{AHY}, F_{AHY}	A categorical variable for the preflood period (2005–2009).	—	—	—	—
Year	NS, $\phi_{prefledging}$, $p_{prefledging}$, S_{HY}, F_{HY}, S_{AHY}, F_{AHY}	A categorical variable for year (2005–2014).	—	—	—	—

[a] Although Catlin et al. (2015) did not detect a relationship between nesting density and nest success or survival and fidelity parameters, we retained the variable because densities postflood were far lower than those prior to the flood.

TABLE 2. Hypotheses and rationale for nest success, prefledging chick apparent survival, after-hatch-year (AHY) true survival and fidelity, and hatch-year (HY) true survival and fidelity of Piping Plovers on the Gavins Point Reach of the Missouri River, USA, 2005–2014.

Demographic parameter	Hypothesis	Rationale
Nest success (NS)	NS would be higher on postflood sandbars, however could decrease as the postflood sandbars aged.	The increased amount of habitat and therefore decreased nesting densities following the flood would lead to lower levels of predation and increased nest success. During the preflood portion of the study, nest success decreased as the engineered sandbars aged because of increased predation (Catlin et al. 2015), which we hypothesized would also be true for the postflood sandbars.
Prefledging apparent chick survival ($\phi_{\text{prefledging}}$)	$\phi_{\text{prefledging}}$ would be higher on postflood sandbars and the effect of density might decrease as chicks aged.	The increased amount of habitat and therefore decreased nesting densities following the flood would lead to lower levels of predation, as well as more foraging habitat available per brood and increased prefledging survival. However, we also hypothesized that the effect of density could decrease as chicks aged and were better able to compete for resources.
HY true survival (S_{HY})	S_{HY} would be higher following the flood.	The increased amount of available habitat would benefit chicks both in the prefledging period (decreased densities) and the following breeding season as they could be more likely to have the ability to set up a territory and breed, therefore potentially increasing HY survival (Catlin et al. 2015).
AHY true survival (S_{AHY})	S_{AHY} would be lower during the flood and higher following the flood.	There is evidence that the survival of nonbreeding Piping Plovers is lower than that of breeding Piping Plovers (Catlin et al. 2015). As all habitat on the Gavins Point Reach was inundated during 2011, many Piping Plovers did not have the opportunity to breed, which may have lowered survival. Following the flood, the increased amount of habitat allowed more individuals to set up territories and breed, which may have increased survival. Survival of AHY birds may also have increased due to decreased predation following the flood. Although many Missouri River shorebird predators key in on nests and prefledging chicks, adults are also likely lost to predators.
HY fidelity (F_{HY})	F_{HY} would be higher following the flood.	With HY Piping Plovers arriving, on average, 28 days after AHY birds (Catlin et al. 2015), the increased amount of habitat available to set up a territory following the flood could have led to higher fidelity to the study area.
AHY fidelity (F_{AHY})	F_{AHY} would be lower during the flood and higher following the flood.	As all of the Gavins Point Reach was inundated during 2011, Piping Plovers had to locate other areas for breeding, therefore decreasing fidelity to the study area. Following the flood, the increased amount of habitat available to set up a territory could have led to higher fidelity to the study area.

detection probability (p) from hatching to fledging (25 days). We modeled age- (days) and year-specific variation in both ϕ and p. We estimated overdispersion using a model that included year- and age-specific variation in apparent survival and detection probability (age*year). Prior to this modeling, using the global model (fully age and year dependent), we tested the addition of an individual random effect on ϕ alone, on p alone, on both ϕ and p, and on neither ϕ nor p. We determined (using AIC_c) that an individual random effect on p improved the fit of the global model, and all modeling proceeded using an individual random effect on p.

We hypothesized that prefledging chick survival would be higher on postflood sandbars (Table 2). We began by modeling basic structures for ϕ and p. We then used the model with the lowest AIC_c value and repeated this process, adding covariates for engineered sandbars, the age of engineered sandbars, and the interaction between nesting density and chick age to ϕ, as well as engineered sandbars and density to p. In the final step, we tested for the effects of the flood using the highest-ranked model from the previous step.

True survival and fidelity to the study area. We estimated Piping Plover annual true survival and fidelity to the study area using the live–dead encounter model, which allowed us to estimate survival unbiased by emigration by using supplementary resightings (from breeding, wintering, and migration locations outside our study area) to separate survival from permanent emigration (Barker 1997). The parameters of the model were true survival (S), detection probability (p), reporting rate of dead encounters (r), detection probability during the supplementary period given that an animal survived (R), probability of being detected and then dying during the supplementary period (R'), fidelity to the study area (F), and probability that an individual returned to the study area after emigrating (F'). As there were no reports of dead plovers outside our study area, we fixed r at 0.

We hypothesized that AHY survival and fidelity would be lowest during the flood and highest following the flood, and that HY survival and fidelity would be higher following the flood (Table 2). We estimated overdispersion using median $\hat{c}$ in a model with year- and age-specific variation for all parameters (except r). We began modeling by testing several reduced structures for p, R, and R', while setting S, F, and F' to be fully time (year) and age (AHY vs. HY) dependent. Based on results of prior modeling (Catlin et al. 2015), we also included the covariates of hatching date and age at banding on HY survival in all models, except when testing for overdispersion. We used the model with the lowest $\mathrm{AIC_c}$ and repeated this process for S, F, and F'. Finally, we tested for effects of engineered sandbars, engineered sandbar age, and nesting density on annual HY true survival and fidelity to the study area, and for effects of the flood on HY and AHY true survival and fidelity.

Reproductive output (RO) and population growth (λ). We estimated the number of fledged chicks produced per pair (reproductive output; RO) using our year-specific estimates of nest success and prefledging chick survival for each habitat type (preflood natural, preflood engineered, and postflood; Appendix B equation 4). To calculate population growth (λ), we used the following equation (Cohen and Gratto-Trevor 2011, Catlin et al. 2015):

$$\lambda = S_{\mathrm{AHY}} + RPBS_{\mathrm{postfledging}} + R(1-P)BS_{\mathrm{AHY}}S_{\mathrm{postfledging}}, \tag{1}$$

where λ represents the population growth rate from year t to year $t+1$, S_{AHY} represents the true survival of AHY birds (directly estimated from our study; Table 3), R represents the sex ratio at hatching (0.50; Cohen and Gratto-Trevor 2011), P represents the probability that a returning HY bird will breed in its first year (0.68; Gratto-Trevor et al. 2010, Cohen and Gratto-Trevor 2011), B represents the birth rate (RO, the number of fledged chicks produced per pair, derived from our study; Table 3), and $S_{\mathrm{postfledging}}$ represents postfledging survival, derived from our study (Table 3) using the equation:

$$S_{\mathrm{postfledging}} = S_{\mathrm{HY}}/\phi_{\mathrm{prefledging}}, \tag{2}$$

where S^{HY} represents HY true survival (directly estimated from our analyses), and $\phi^{\mathrm{prefledging}}$ represents the apparent survival of chicks from hatching to fledging (directly estimated from our analyses).

The first part of equation 1 refers to breeding females that survived from year t to year $t+1$. The second part of equation 1 refers to new females that were recruited in year $t+1$ from year t (the current year), and the third part of the equation refers to new females that were recruited into the breeding population in year $t+1$ from year $t-1$ that were not recruited in their first year posthatch. To calculate the reproductive output needed for a stationary population, we set $\lambda = 1$ and solved the equation for B (assuming $B_t = B_{t-1}$; Cohen and Gratto-Trevor 2011, Catlin et al. 2015). We incorporated variance into the model by obtaining the estimate of process variance (process variance [σ^2] = total variance − sampling variance) for AHY true survival (Gould and Nichols 1998, Larson et al. 2000).

RESULTS

We monitored 1,071 nests and banded 986 AHY Piping Plovers and 2,021 prefledging chicks from 2005 to 2014. Chicks were banded at 1.80 (range: 0–24) days of age and had a mean hatching date of June 27 (range: May 26–August 4). The average density of nests on sandbars was 1.16 (range: 0.01–12.75) pairs ha^{-1}. Thirty-nine percent of banded AHY birds (389/986) and 11% of banded chicks (222/2,021) were observed outside the study area during the supplementary period. The amount of available suitable habitat varied between years, with more habitat available after the flood ($\bar{x}_{\mathrm{postflood}} = 1{,}012$ ha, range: 887–1,103 ha; Table 3) than before the flood ($\bar{x}_{\mathrm{preflood}} = 166$ ha, range: 98–307 ha), which resulted in lower nesting densities after the flood ($\bar{x}_{\mathrm{postflood}} = 0.20$ pairs ha^{-1}, range: 0.11–0.36 pairs ha^{-1}; Table 3) than before the flood ($\bar{x}_{\mathrm{preflood}} = 1.22$ pairs ha^{-1}, range: 0.74–2.11 pairs ha^{-1}).

Nest Success

Nest success to 34 days averaged 0.52 ± 0.02 SE from 2005 to 2014, and was higher in postflood habitat (0.74 ± 0.02 SE, $n = 270$) than in preflood habitat (0.45 ± 0.02 SE, $n = 801$). Our top model (Appendix A Table 4) indicated that daily nest survival was positively related to the use of

TABLE 3. Estimated demographic parameters, available nesting habitat, and nesting density for after-hatch-year (AHY) and hatch-year (HY) Piping Plovers on the Gavins Point Reach of the Missouri River, USA, 2005–2014. Estimates are presented as $\bar{x} \pm 1$ SE unless otherwise noted.

Year	Nest success [a]	Apparent prefledging chick survival (ϕ) [b]	AHY true survival (S_{AHY}) [c,d,e]	HY true survival (S_{HY}) [c,d]	AHY fidelity (F_{AHY}) [c,d]	HY fidelity (F_{HY}) [c,d]	Postfledging survival ($S_{postfledging}$) [d,e,f]	Reproductive output (RO; chicks pair^{-1}) [e,g]	Area (ha) [h]	Density (pairs ha^{-1}) [i]
2005	0.50 ± 0.02	0.66 ± 0.05	0.83 ± 0.04	0.23 ± 0.03	0.94 ± 0.02	0.74 ± 0.07	0.43 ± 0.03	1.63 ± 0.04	161.34	1.02 ± 0.78
2006	0.48 ± 0.01	0.32 ± 0.03	0.81 ± 0.03	0.17 ± 0.03	0.87 ± 0.03	0.52 ± 0.08	0.43 ± 0.04	0.76 ± 0.03	138.15	0.96 ± 1.10
2007	0.49 ± 0.02	0.15 ± 0.02	0.80 ± 0.02	0.18 ± 0.03	0.95 ± 0.02	0.75 ± 0.10	0.47 ± 0.04	0.36 ± 0.02	98.05	1.25 ± 1.01
2008	0.47 ± 0.02	0.56 ± 0.04	0.77 ± 0.03	0.17 ± 0.03	0.95 ± 0.02	0.75 ± 0.06	0.32 ± 0.02	1.30 ± 0.02	306.66	0.74 ± 1.01
2009	0.34 ± 0.01	0.28 ± 0.03	0.68 ± 0.03	0.06 ± 0.02	0.92 ± 0.02	0.64 ± 0.09	0.21 ± 0.03	0.54 ± 0.03	127.94	2.11 ± 2.99
2010 [j]	—	—	0.72 ± 0.03	—	0.89 ± 0.03	—	—	—	—	—
2011 [j]	—	—	0.75 ± 0.05	—	0.76 ± 0.05	—	—	—	—	—
2012	0.78 ± 0.02	0.63 ± 0.04	0.72 ± 0.05	0.49 ± 0.04	0.93 ± 0.03	0.64 ± 0.07	0.71 ± 0.07	1.94 ± 0.05	1,046.18	0.11 ± 0.19
2013	0.76 ± 0.02	0.70 ± 0.03	0.78 ± 0.03	0.43 ± 0.04	0.98 ± 0.02	0.88 ± 0.08	0.56 ± 0.04	2.12 ± 0.04	1,103.28	0.13 ± 0.11
2014 [k]	0.71 ± 0.02	0.61 ± 0.02	—	—	—	—	—	1.78 ± 0.03	886.56	0.35 ± 0.55

[a] Nest success was calculated using a random effects logistic exposure model (Rotella et al. 2000, Shaffer 2004, Stephens et al. 2004).
[b] Apparent prefledging chick survival (ϕ) was calculated using a random effects Cormack-Jolly-Seber model (Gimenez and Choquet 2010).
[c] S_{AHY}, S_{HY}, F_{AHY}, and F_{HY} were calculated using a Barker (1997) model.
[d] Estimates for S_{AHY}, S_{HY}, F_{AHY}, F_{HY}, and $S_{postfledging}$ represent survival and fidelity to the study area from one breeding season to the next. For example, S_{AHY} in 2005 represents AHY true survival from 2005 to 2006.
[e] Estimates used to calculate population growth (λ).
[f] $S_{postfledging}$ was calculated using $S_{HY}/\phi_{prefledging}$.
[g] RO was calculated using Equation 4 (Appendix B).
[h] Area (ha) represents the amount of available suitable (sparsely vegetated and unvegetated) habitat throughout the study duration.
[i] Density (pairs ha^{-1}) represents the nesting density calculated from the maximum number of active nests divided by the amount of suitable available habitat.
[j] 2010 and 2011 represent years where flooding inundated all nesting habitat on the Gavins Point Reach and resulted in no nests hatching or chicks surviving.
[k] S_{AHY}, S_{HY}, F_{AHY}, F_{HY}, and $S_{postfledging}$ were not estimable in the final year of the study (2014).

predator exclosures during the preflood period, preflood engineered habitat, the date of nest initiation, clutch size, and postflood habitat, and negatively related to the age of the nest and the age of preflood engineered habitat (Appendix A Table 5). Our top model did not include nesting density and the age of postflood sandbars, indicating that these factors were less important for determining Piping Plover daily nest survival in our study than the other variables examined.

Prefledging Chick Survival

Prefledging chick survival (ϕ) to 25 days varied among years and by chick age throughout the duration of the study and was consistently higher after the flood (2012–2014; Table 3). The 2 highest-ranked models for daily chick survival (cumulative $w_i = 0.76$) included the interaction between year and age, hatching date, engineered habitat, and the interaction between density and age (Appendix A Table 6). Our top model (Appendix A Table 6) indicated that daily chick survival was negatively related to hatching date and the age of engineered habitat and positively related to hatching on engineered habitat and the interaction between chick age and density, although the confidence interval included 0 for the effect of engineered habitat and age of engineered habitat (Appendix A Table 7). Detection probability (p) varied by year and chick age (Appendix A Table 6) and was higher on sandbars with higher nesting densities and on engineered sandbars, although the confidence interval for engineered habitat included 0 (Appendix A Table 7).

True Survival and Fidelity to the Study Area

AHY true survival (S) averaged 0.76 ± 0.05 SE throughout the study, and the top model (Appendix A Table 8) indicated that true survival varied between the preflood, flood, and postflood periods, such that it was highest prior to the flood, lowest during the flood, and intermediate after the flood (Table 3). There was also some indication that AHY true survival varied by year, as evident by the second-ranked model (Appendix A Table 8). AHY true survival was higher than HY true survival in each year of the study, and HY true survival was highest following the flood (Table 3). HY true survival was positively related to the age of chicks at banding and engineered habitat and negatively related to hatching date, nesting density (Figure 3), and the age of engineered habitat, although the confidence interval for the age of engineered habitat overlapped 0, suggesting that it was a not significant factor (Appendix A Table 9).

Our top model (Appendix A Table 8) indicated that fidelity to the study area (F) varied by year and age. Fidelity was higher for AHY birds than for HY birds in all years of the study, and HY fidelity was highest from 2013 to 2014 (Table 3). Fidelity to the study area was lowest for AHY birds from 2011 to 2012 (Table 3) and highest from 2013 to 2014. The probabilities of being detected in our study area (p), subsequently dying during the supplementary period (R'), and returning to the study area after emigrating (F') did not vary by year (Appendix A Table 8) and were lower for HY birds than for AHY birds ($\beta = -1.75 \pm 0.3$ SE, $\beta = -3.10 \pm 0.57$ SE, and $\beta = -0.81 \pm 0.66$ SE, respectively). The probability of being resighted outside the study area (R) varied among years and ages (Appendix A Table 8) and was lower for HY birds than for AHY birds ($\bar{x}_{\mathrm{HY}} = 0.19 \pm 0.08$ SE vs. $\bar{x}_{\mathrm{AHY}} = 0.25 \pm 0.08$ SE).

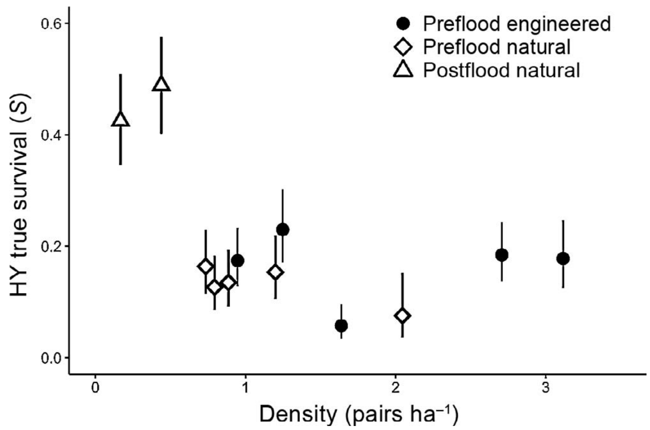

FIGURE 3. Survival of hatch-year (HY) Piping Plover chicks (from hatching to the following breeding season) in relation to nesting density. Estimates are from chicks that hatched on the Gavins Point Reach of the Missouri River, USA, prior to flooding (2005–2009; preflood engineered and preflood natural sandbar habitat), and following a flood event in 2011 (2012–2014; postflood natural sandbar habitat). Estimates and standard errors are derived from model-averaged parameter estimates and unconditional standard errors from models of HY survival. Error bars represent 95% confidence intervals.

Reproductive Output and Population Growth

The reproductive output needed for a stationary population given observed survival rates was 1.17 chicks fledged per pair (95% CI: 0.74–1.70). Prior to the flood, reproductive output only exceeded that needed for a stationary population in 2 yrs; however, following the flood, reproductive output was as high as or higher than that of engineered habitat and was above that needed for a stationary population in all years (Figure 4). Prior to the flood, calculated λ exceeded 1 in only 1 yr (Figure 5). Lambda was lowest and substantially less than 1 during the years of the flood, when reproductive output was 0, and was highest after the flood, exceeding 1 in all years (Figure 5).

DISCUSSION

On the Missouri River, a byproduct of managing for flood control has been the dramatic alteration of the ecosystem,

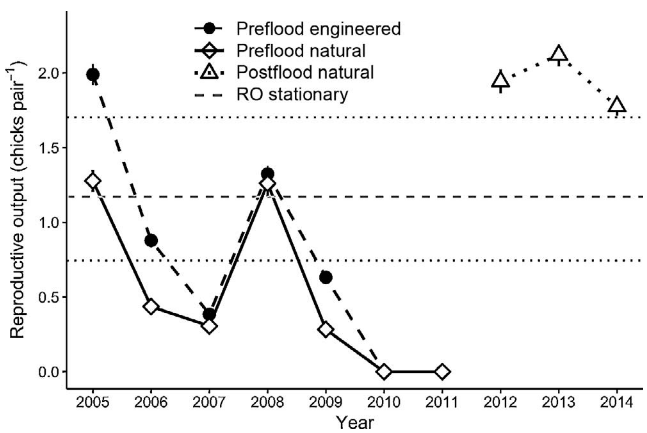

FIGURE 4. Estimated Piping Plover reproductive output (chicks pair^{-1}) on the Gavins Point Reach of the Missouri River, USA, prior to flooding, 2005–2009 (preflood engineered and preflood natural sandbar habitat), and following flooding, 2012–2014 (postflood natural sandbar habitat). The estimated reproductive output (RO) needed for a stationary population is indicated by the dashed gray line and the 95% confidence limits by the dotted black lines. Error bars represent 95% confidence intervals.

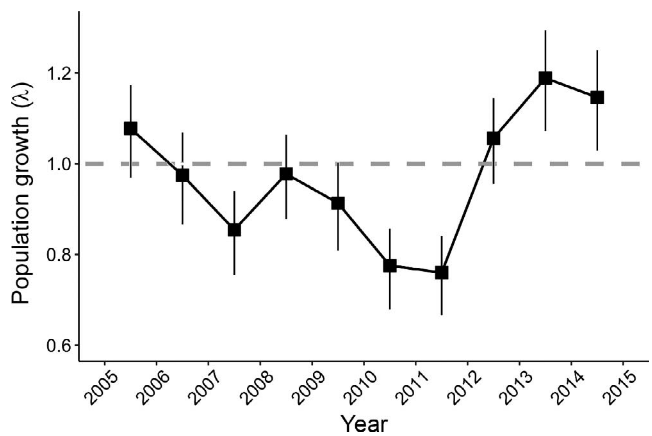

FIGURE 5. Estimated population growth (λ) of Piping Plovers nesting on the Gavins Point Reach of the Missouri River, USA, 2005–2014. λ was derived from our demographic models. The dashed line represents stationarity (λ = 1), and error bars represent 95% confidence intervals.

leading to decreases in a variety of taxa, primarily due to habitat loss (U.S. Fish and Wildlife Service 2003, Dixon et al. 2012, Catlin et al. 2015, Johnson et al. 2015). When the Missouri River flooded in 2010 and 2011, there was extensive damage to human infrastructure (NOAA 2012), but the floodwaters also increased the amount of Piping Plover nesting habitat substantially, contributing to a decline in nesting densities and increases in almost all measured demographic rates.

Estimates of nest success, prefledging chick survival, and HY annual survival were as high or higher after the flood than before, and, unlike prior to the flood, these rates remained high as the sandbar habitat aged. Increased nest, chick, and HY survival following the flood resulted in high reproductive output and population growth. Suitable habitat increased and nesting densities decreased following the flood, and our results indicated that both prefledging chick survival and HY survival were density dependent. As HY survival was calculated from hatching to the following breeding season, it is likely that some component of density-dependent HY survival was influenced by the importance of nesting density during the prefledging period. On the Missouri River, decreased nesting densities can result in increased availability of foraging habitat for individuals (Catlin et al. 2013, 2014), decreased predation (Catlin et al. 2015), and decreased inter- and intra-species aggression (D. H. Catlin personal observation). Moreover, lower densities were related to a higher proportion of double brooding (Hunt et al. 2015), which may also increase reproductive output. Our results indicated that these fecundity parameters, coupled with increased immigration (Catlin et al. 2016), drove the growth of the population following the flood.

Annual AHY true survival was relatively high (0.76 ± 0.05) throughout the study and was similar to what has been reported from other Piping Plover breeding locations (reviewed by Catlin et al. 2015). AHY true survival was lowest during the flood, which may be attributable to nonbreeding Piping Plovers exhibiting lower survival than breeding Piping Plovers (Catlin et al. 2015, Weithman et al. in press). With all sandbar habitat on the Gavins Point Reach inundated during the flood (2011), many individuals did not have the opportunity to breed, while others dispersed elsewhere (Catlin et al. 2016), leading to the lowest AHY fidelity that we observed. Of those that moved to other breeding locations (the few sandbars that remained above water), many experienced catastrophic nest failure (Catlin et al. 2015). Breeding habitat away from river systems may be especially important following flood events (Catlin et el. 2016, Roche et al. 2016, Zeigler et al. 2017). Similarly, in Saskatchewan, Roche et al. (2012) found that Piping Plovers were more likely to disperse from a breeding area when they experienced flooding and low reproductive success in the previous year. These results suggest that plovers are adapted to flooding and related nest failure, and will move to improve their breeding prospects, and our results suggest that, in particular, when flooding creates habitat, they can capitalize on it relatively quickly.

The mechanical creation of habitat from 2004 to 2009 increased reproductive output and contributed to positive population growth for a year following creation. Immediately after construction, Piping Plovers selected engineered habitat over natural habitat (Catlin et al. 2011b). However, immigration and reproductive rates decreased rapidly as density increased, and, even with the construction of sandbar habitat, Piping Plovers were at or near carrying capacity throughout the preflood portion of this study (Catlin et al. 2015). In comparison, flooding increased the amount of suitable habitat, resulting in lower densities and ultimately high population growth. Although available habitat decreased between 2013 and 2014, reproductive output remained high, suggesting that the population was below carrying capacity. On average, HY Piping Plovers arrived 28 days after AHY birds (Catlin et al. 2015) and, with the population near carrying capacity, these individuals may have lost the ability to secure a territory and therefore may have exhibited decreased fidelity to the study area and potentially decreased survival (Catlin et al. 2015). After the flood, annual HY true survival and fidelity to the study area increased.

Across their range, Piping Plovers rapidly colonize newly created suitable habitat (Wilcox 1959, Cohen et al. 2009, Catlin et al. 2015). Our results indicated that Piping Plovers experienced increased reproductive output and population growth in the habitat created by the 2011 flood. Remarkably, these gains in reproductive output were achieved without predator management, compared with intensive predator management on engineered sandbars prior to the flood (Catlin et al. 2015). Nest exclosures and predator removal are commonly used to protect beach-nesting birds (U.S. Fish and Wildlife Service 1985, 2009, Johnson and Oring 2002, Neuman et al. 2004, Niehaus et al. 2004, Isaksson et al. 2007, Cohen et al. 2009, Catlin et al. 2011b). Indeed, use of exclosures prior to the flood on the Missouri River increased nest success, and Great Horned Owl removal increased chick survival in 1 of 2 yr studied (Catlin et al. 2011a, 2015). Small parcels of habitat and high nesting densities before the flood may have facilitated predation prior to the flood (Burger 1984, Catlin et al. 2015). Nests and chicks were still lost to predators following the flood, but predation was substantially reduced, suggesting that Piping Plover nest and chick predation were density-dependent during our study. Kruse et al. (2001) suggested that predator efficiency would be reduced on large sandbars with large areas of unused nesting habitat. It is also possible that predators such as mink, raccoons, and coyotes experienced decreased survival during the flood, resulting in lower populations of these species postflood.

Piping Plovers are representative of a suite of Charadriiformes that breed in riparian ecosystems and are affected by anthropogenic alterations. In New Zealand, a number of species, including the critically endangered Black Stilt (*Himantopus novaezelandiae*) and the threatened Wrybill (*Anarhynchus frontalis*), breed in braided river ecosystems on both gravel bars and in wetlands which are affected by the presence of hydroelectric dams (Caruso 2006a, 2006b). In Japan, dam construction and subsequent flood regulation on the Tama River has resulted in the loss of gravel bar habitat and the invasion of exotic plants, ultimately affecting breeding Long-billed Plovers (*Charadrius placidus*; Katayama et al. 2010). Along the Mekong River in northeastern Cambodia, sandbar-nesting species such as the River Lapwing (*Vanellus duvaucelii*) and Little Ringed Plover (*Charadrius dubius*) are affected by the Yali Falls dam, resulting in inundated nests and drowned chicks and loss of breeding and foraging habitat (Claassen 2004). Similarly to the Missouri River, habitat management strategies such as vegetation removal and wetland and gravel bar creation have been implemented with generally positive results, including birds returning to restored areas and increased nesting pairs and nest success (Caruso 2006b, Katayama et al. 2010). However, successful management practices such as these are expensive and often difficult to maintain (Caruso 2006b, Catlin et al. 2015).

Although our results suggest that flood-created habitat resulted in improved demographic outcomes for Piping Plovers, management will likely continue to focus on creating engineered sandbar habitat. Thus, it will be imperative for managers to use what has been learned to improve engineering efficiency and maximize benefits for Piping Plovers. The amount of habitat affected population growth, so building more habitat at one time may provide a better outcome than smaller projects. Not only does the amount of habitat matter, but its proximity to existing sources of birds is also important. Piping Plovers on the Missouri River and elsewhere exhibit relatively high site fidelity between years, with young prospecting locally for their first nesting locations (Catlin et al. 2015, Friedrich et al. 2015, Davis et al. 2017), and exchange among local breeding populations is relatively low (Catlin et al. 2016). These pieces of evidence indicate that the future construction of sandbar habitat should be in close proximity to the already existing postflood sandbars on the Gavins Point Reach. Catlin et al. (2015) suggested that sandbars be built within 12 km of source populations to capture population growth locally. Our results suggest that, in addition, habitat quantity be taken into account, maximizing the amount of habitat created while balancing environmental and economic considerations. Regardless of the path taken moving forward, Piping Plovers likely will not reach a stage where management actions are no longer necessary unless we dramatically alter the way in which we manage our rivers using controlled flooding.

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APPENDIX A

APPENDIX A TABLE 4. Model selection for a random effects logistic exposure model (Rotella et al. 2000, Shaffer 2004, Stephens et al. 2004) for daily survival rate (DSR) of Piping Plovers (*Charadrius melodus*) on the Gavins Point Reach of the Missouri River, 2005–2014.

Step [a]	Model [b]	K [c]	ΔAIC_c [d]	Deviance [e]	w_i [f]
3	Postflood [g] + Exclosure + Date + Age + Clutch size + Engineered + Engineered age + Random effect [h]	9	0.00	4,333.70	0.60
4	Postflood [g] + Exclosure + Date + Age + Clutch size + Engineered + Engineered age + Postflood age + Random effect	10	1.70	4,333.40	0.26
2	Year + Exclosure + Date + Age + Clutch size + Engineered + Engineered age + Random effect	15	3.70	4,325.40	0.09
1 [i]	Year + Exclosure + Date + Age + Clutch size + Engineered + Engineered age + Density + Random effect	16	5.00	4,324.60	0.05

[a] The staged approach used when modeling nest success.
[b] Descriptions of variables used can be found in Table 1.
[c] Number of parameters in the model.
[d] The difference from the top model in Akaike's information criterion corrected for small sample size (AIC_c) (minimum AIC_c = 4,351.70).
[e] Model deviance.
[f] The relative weight of evidence for each model.
[g] Preflood was used as the reference variable.
[h] Random effect of sandbar within a given year to account for the dependence of nests on a given sandbar in a given year.
[i] The global model obtained from Catlin et al. (2015), with the addition of the density variable as nesting densities were substantially lower following the flood.

APPENDIX A TABLE 5. β estimates and 95% confidence limits (95% CL) from the top-ranked model (Appendix A Table 4) for the effect of variables on daily survival rate (DSR) from a random effects logistic exposure model (Rotella et al. 2000, Shaffer 2004, Stephens et al. 2004) for Piping Plover nests on the Gavins Point Reach of the Missouri River, 2005–2009 and 2012–2014.

Variable [a]	Estimate	SE	Estimate/SE [b]	Lower 95% CL	Upper 95% CL
Intercept	2.07	0.20	10.23	1.67	2.47
Postflood	1.60	0.21	7.54	1.18	2.02
Exclosure	0.74	0.13	5.53	0.48	1.01
Date	0.01	0.01	2.89	0.00	0.01
Age	−0.01	0.01	−1.67	−0.02	0.01
Clutch size	0.27	0.04	6.73	0.19	0.35
Engineered	1.33	0.31	4.29	0.72	1.94
Engineered age	−0.41	0.12	−3.46	−0.65	−0.18
Random effect [c]	0.55	0.14	4.03	0.28	0.82

[a] Descriptions of variables can be found in Table 1.
[b] The size of the effect relative to the SE.
[c] Random effect of sandbar within a given year to account for the dependence of nests on a given sandbar in a given year.

APPENDIX A TABLE 6. Model ranking results for random effects Cormack-Jolly-Seber models (Gimenez and Choquet 2010) of apparent survival (ϕ) and detection probability (*p*) of prefledging Piping Plover chicks on the Gavins Point Reach of the Missouri River, 2005–2009 and 2012–2014. An individual random effect was estimated for *p* in each model.

ϕ [a]	*p* [a]	*K* [b]	ΔAIC_c [c,d]	w_i [e]	Dev [f]
Age*Year + Hatch + Engineered + Engineered age + Density*Age	Age*Year + Engineered + Density	224	0.00	0.44	23,162.18
Age*Year + Hatch + Engineered + Density*Age	Age*Year + Engineered + Density	223	0.63	0.32	23,164.91
Age*Year + Hatch + Engineered + Engineered age	Age*Year + Engineered + Density	222	2.41	0.13	23,168.78
Age*Year + Hatch + Engineered	Age*Year + Engineered + Density	221	2.81	0.11	23,171.28

[a] Descriptions of variables used can be found in Table 1.
[b] Number of parameters in the model.
[c] The difference from the top model in Akaike's information criterion corrected for small sample size (minimum $AIC_c = 23{,}620.98$).
[d] Models were corrected for overdispersion ($\hat{c} = 1.06$).
[e] The relative weight of evidence for each model.
[f] Model deviance.

APPENDIX A TABLE 7. β estimates and 95% confidence limits (95% CL) from the top-ranked model (Appendix A Table 6) for the effects of individual covariates on apparent survival (ϕ) and resighting or detection probability (*p*) from a random effects Cormack-Jolly-Seber (Gimenez and Choquet 2010) analysis of prefledging Piping Plover chicks on the Gavins Point Reach of the Missouri River, 2005–2009 and 2012–2014.

Parameter	Variable [a]	Estimate	SE	Estimate/SE [b]	Lower 95% CL	Upper 95% CL
Apparent survival (ϕ)	Hatch	−0.02	0.01	−6.86	−0.03	−0.02
	Engineered	0.02	0.14	0.12	−0.26	0.30
	Engineered age	−0.08	0.05	−1.67	−0.17	0.02
	Density*Age	0.01	0.01	2.32	0.01	0.03
Detection probability (*p*)	Engineered	0.10	0.11	0.95	−0.11	0.32
	Density	0.09	0.03	2.93	0.03	0.15

[a] Descriptions of variables can be found in Table 1.
[b] The size of the effect relative to the SE.

APPENDIX A TABLE 8. Model ranking results for Barker (1997) models of true survival (*S*), resighting probability (*p*), probability of being resighted during and surviving the supplementary period (breeding, migration, and wintering locations outside our study area; *R*), probability of being resighted and then dying during the supplementary period (*R′*), fidelity of individuals to the study area (*F*), and return rate of individuals that had emigrated (*F′*) for after-hatch-year (AHY) and hatch-year (HY) Piping Plovers on the Gavins Point Reach of the Missouri River, 2005–2014.

S [a]	*F* [a]	*K* [b]	ΔAIC_c [c,d]	w_i [e]	Dev [f]
HY(Band age + Hatch) + Age + Age*(Postflood[g] + Flood) + HY(Engineered + Engineered age + Density)	Age + Yr	41	0.00	0.16	10,136.60
HY(Band age + Hatch) + AHY(Yr2 + Yr3 + Yr4 + Yr5 + Yr6 + Yr7 + Yr8 + Yr9 + Yr10) + Age + HY(Postflood + Flood + Engineered + Engineered age + Density)	Age + Yr + HY(Engineered)	49	0.68	0.11	10,121.05
HY(Band age + Hatch) + AHY(Yr2 + Yr3 + Yr4 + Yr5 + Yr6 + Yr7 + Yr8 + Yr9 + Yr10) + Age + HY(Postflood + Flood + Engineered + Engineered age + Density)	Age + Yr + HY(Engineered + Engineered age)	50	0.92	0.10	10,119.25
HY(Band age + Hatch) + AHY(Yr2 + Yr3 + Yr4 + Yr5 + Yr6 + Yr7 + Yr8 + Yr9 + Yr10) + Age + HY(Postflood + Flood + Engineered + Density)	Age + Yr + HY(Engineered + Engineered age)	49	1.27	0.09	10,121.64
HY(Band age + Hatch) + Age + Age*(Postflood[g] + Flood) + HY(Engineered + Engineered age + Density)	Age + Yr + HY(Density)	42	1.81	0.07	10,136.38

[a] Descriptions of variables used can be found in Table 1. HY() indicates that the variables within the parentheses only affected HY Piping Plovers. All models with $w_i > 0.01$ had the same variables for the following parameters: $p =$ Age; $R' =$ Age; $F' =$ Age; $R =$ Age*Yr.
[b] Number of parameters in the model.
[c] The difference from the top model in Akaike's information criterion corrected for small sample size (minimum AIC_c =10,219.18).
[d] Models were corrected for overdispersion ($\hat{c} = 1.13$).
[e] The relative weight of evidence for each model.
[f] Model deviance.
[g] Preflood was used as the reference variable in this model.

APPENDIX A TABLE 9. β estimates and 95% confidence limits (95% CL) from the top-ranked model (Appendix A Table 8) for the effect of individual covariates on annual true survival (*S*) from a Barker (1997) model for hatch-year (HY) Piping Plovers on the Gavins Point Reach of the Missouri River, 2005–2009 and 2012–2014.

Parameter	Variable [a]	Estimate	SE	Estimate/SE [b]	Lower 95% CL	Upper 95% CL
True survival (*S*)	Hatch	−0.046	0.006	−7.733	−0.057	−0.034
	Band age	0.114	0.031	3.686	0.053	0.175
	Engineered	0.710	0.240	2.964	0.240	1.179
	Engineered age	−0.215	0.110	−1.949	−0.432	0.001
	Density	−0.227	0.099	−2.305	−0.421	−0.034

[a] Descriptions of variables used in the models can be found in Table 1.
[b] The size of the effect relative to the SE.

APPENDIX B

Equations Used to Calculate Nest Success and Reproductive Output (RO) of Piping Plovers on the Gavins Point Reach of the Missouri River, 2005–2009 and 2012–2014

Equation 3. Nest success

$$\mathrm{DSR}_i = \frac{e^{\beta_0 + \sum_j \beta_j x_{ij}}}{1 + e^{\beta_0 + \sum_j \beta_j x_{ij}}},$$

where i represents the day, j represents the covariate, and β_j represents the coefficient of covariate j.

Equation 4. Reproductive output

$$\text{Chicks pair}_{i,t}^{-1} = \mathrm{CS} \times \mathrm{FS}_{i,t} \times \phi_{\text{prefledging } i,t} + (1 - \mathrm{FS}_{i,t}) \times (\mathrm{CS} \times \mathrm{FS}_{i,t} \times \phi_{\text{prefledging } i,t}),$$

where i represents the habitat type (preflood natural, preflood engineered, or postflood), t represents the year, CS represents clutch size (mean size of completed clutches in our study = 3.73; Catlin et al. 2015), $\phi_{\text{prefledging}}$ represents the survival of chicks from hatching to fledging (directly estimated from our analyses), and FS represents the probability that a female successfully hatched eggs in a given year. In the Great Lakes, the estimated renesting probability was 50% (Claassen et al. 2014); however, we didn't have renesting probabilities for our population. We used the following equation for female success (FS) to account for nesting attempts following nest failure (Cowardin and Johnson 1979):

$$\mathrm{FS} = \text{Nest success} \times e^{(1-\text{Nest success})^2}.$$