

Population Dynamics of Piping Plovers (*Charadrius melodus*) on the Missouri River

Daniel Herbert Catlin

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James Fraser (Chair)
James Berkson
Eric Hallerman
Marcella Kelly
Jeffrey Walters

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ABSTRACT

Habitat loss and predation are threatening many shorebird populations worldwide. While habitat preservation often is preferable, sometimes habitat needs to be restored or created in order to stave off immediate declines. The Great Plains population of piping plovers (*Charadrius melodus*) was listed as threatened in 1986, and habitat loss and predation appear to be limiting the growth of this population. On the Missouri River, piping plovers nest on sandbars, but the damming of the mainstem of the Missouri in the mid-twentieth century reduced the natural capacity of the Missouri River to create sandbar habitat. In 2004, the United States Army Corps of Engineers (USACE) implemented a habitat creation project on the Gavins Point Reach of the Missouri River (stretch of river immediately downriver from the Gavins Point Dam) in an effort to promote recovery of piping plovers and the endangered least tern (*Sternula antillarum*). The USACE built 3 sandbars in 2004 – 2005 and built another sandbar on Lewis and Clark Lake in 2007. We studied the population dynamics of piping plovers in relationship to this newly engineered habitat. We monitored 623 nests on 16 sandbar complexes, to evaluate habitat selection, determine the factors affecting nesting success, and compare nesting success between natural and engineered habitat. From these 623 nests, we banded 357 adults and 685 chicks to investigate the factors affecting adult and juvenile survival. We used a logistic-exposure model to calculate nest survival. Adult and juvenile survival was calculated using Cormack-Jolly-Seber based models in Program MARK. We used the estimates from these studies to create a matrix population model for piping plovers nesting on the Gavins Point Reach. We used this model to predict the effects of engineered habitat the on population growth rate.

Piping plovers selected for engineered sandbars and against natural and natural/modified habitats. Daily survival rate (DSR) on engineered habitats was

significantly higher than on natural or natural modified habitats (log odds: 2.71, 95% CI: 1.20 – 6.08). Predator exclosures around nests did not affect DSR after controlling for the effects of date, nest age, and clutch size. Piping plover juvenile survival to recruitment was negatively related to nesting density on the relatively densely populated engineered sandbars. On the less dense natural sandbars, survival to recruitment was positively correlated with density. Adult survival did not appear to be related to density within our study. Movement within the study area was related also to density. Juveniles from densely populated engineered sandbars were more likely to leave engineered habitat to nest on natural sandbars than were juveniles hatched on less densely populated engineered sandbars. Movements among sandbars by breeding adults suggested that adults preferred engineered habitat. It is possible that juveniles moved to natural habitats because they were unable to compete with adults for the more desirable engineered habitats. Adults and juveniles emigrated from the study area at a higher rate after the 2006 breeding season, a year when water discharge was higher, nesting densities were higher, and reproductive success was lower (as a result of predation) than in the other years. Deterministic modeling suggested that engineered habitat significantly increased population growth. Decreased productivity over time and associated predicted negative population growth suggest that the amount of engineered habitat created was inadequate to sustain population growth, and/or that relatively high water discharge and nesting densities coupled with low reproductive rates and high emigration rates could lead to rapid declines in the plover population. Continued research is needed to determine the effects of these factors on long-term population growth. Our results suggest that habitat creation could be a viable short-term solution to population declines in shorebird populations limited by habitat loss, but high densities and increased predation associated with habitat creation indicate that other, long-term solutions may be required.

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INTRODUCTION

The piping plover (*Charadrius melodus*) is a small shorebird that nests on open sand and gravel habitats on the east coast of North America, the Great Lakes, and on the Great Plains of the United States and Canada. The Great Plains piping plover population was listed as threatened under the Endangered Species Act in 1986. One of the major threats faced by these birds, particularly those nesting on the Missouri River, is the loss of habitat associated with the damming of the mainstem of the Missouri in the mid-twentieth century. As a result, much of the river was lost under reservoirs, and the remaining riverine stretches experienced substantial changes from the historical flows and sediment loads. Piping plovers use inter-channel, largely unvegetated sandbars for nesting and raising young. Decreases in flows and sediment loads have reduced the frequency of sandbar generation. High flows during the mid-1990s that created large amounts of sandbar habitat illustrated the effect of these changes on piping plovers; piping plover populations on the Missouri River expanded quickly in response to the increased habitat availability.

In 2004 the United States Army Corps of Engineers (USACE) began a habitat creation project in an attempt to mitigate the effects of habitat loss and to meet habitat goals laid out in the United States Fish and Wildlife Service's (USFWS) biological opinion. Initially, three sandbar complexes were created on the Gavins Point Reach in 2004, and in 2007, another sandbar complex was created in the headwaters of Lewis and Clark Lake (a reservoir impounded by the Gavins Point Dam). The overall objective of this study was to evaluate the effects of engineered habitat on the population dynamics of piping plovers on the Missouri River and to evaluate the short-term contributions to population recovery made by these sandbars.

The evaluation of a habitat creation or modification project for breeding birds involves several steps. The first level of evaluation should be habitat use. If a bird population does not use the habitat at least in proportion to its availability, then these habitats probably will not make a significant contribution to conservation. Assuming that the birds do use the habitat, then we should evaluate the population dynamics of these birds as compared to those using existing habitat. Birds nesting on created or modified habitat could have different nesting success, juvenile survival, adult survival,

immigration, or emigration than birds nesting on naturally formed habitat. While finding differences in these parameters among habitat types could help direct future management, the ultimate evaluation of these actions is to assess the effects of engineered habitats on potential population trajectory and recovery. Beyond parameter estimation and determination of the effect-sizes, managers must investigate the contributions of actions to the ultimate goal of recovery.

In the following chapters, we used the above steps to evaluate the effects of the USACE's habitat creation project with data from the first 3 – 4 years following creation.

Chapter 1: Evaluation of habitat selection and nesting success on engineered and natural sandbars,

Chapter 2: Evaluation of adult and juvenile survival and movement on engineered and natural sandbars, and

Chapter 3: Population growth rate with reference to the effects of engineered habitat.

The contents of this dissertation include a portion of the work conducted on the Gavins Point Reach and Lewis and Clark Lake from 2005 – 2007. The remainder of the work will be published subsequently. A partial list of the topics to follow are:

1. Growth rates of pre-fledging piping plovers in relationship to engineered habitat and water discharge,
2. Insect abundance on engineered and natural sandbars and the effects of management actions on food abundance,
3. The factors affecting pre-fledging chick survival in relationship to habitat creation,
4. The effect of owl trapping on pre-fledging chick survival,
5. Piping plover dispersal patterns and the factors affecting dispersal in relationship to habitat creation,
6. Age of fledging for hatchling piping plovers and the effects of food availability and water discharge on timing of fledging,
7. Winter survival of piping plovers on the South Texas coast, and
8. Within-season survival of adult piping plovers on natural and engineered sandbars.

Chapter 1: Piping Plover Phenology, Nest-Site Selection, and Nest Success on Natural
and Engineered Sandbars

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Piping Plover Phenology, Nest-Site Selection, and Nest Success on Natural and Engineered Sandbars

DANIEL H. CATLIN¹, *Department of Fisheries and Wildlife Sciences, Virginia Polytechnic Institute and State University, Blacksburg, VA, 23161, USA*

JAMES D. FRASER, *Department of Fisheries and Wildlife Sciences, Virginia Polytechnic Institute and State University, Blacksburg, VA, 23161, USA*

JOY H. FELIO, *Department of Fisheries and Wildlife Sciences, Virginia Polytechnic Institute and State University, Blacksburg, VA, 23161, USA*

JONATHAN B. COHEN, *Department of Fisheries and Wildlife Sciences, Virginia Polytechnic Institute and State University, Blacksburg, VA, 23161, USA*

ABSTRACT Loss of breeding habitat and nest predation have contributed to the decline of many shorebird species. The United States Army Corps of Engineers (USACE) initiated a piping plover (*Charadrius melodus*) habitat creation and augmentation program on the Missouri River in the summer of 2004. The USACE increased unvegetated sandbar habitat by depositing dredged material and by clearing vegetation from existing sandbars. We evaluated the effects of this increase in nesting and foraging habitat on the nesting behavior and nest daily survival rate (DSR) of piping plovers using these habitats on Lewis and Clark Lake and the Gavins Point Reach of the Missouri River from 2005 – 2007 ($n = 623$ nests). Piping plovers selected engineered sandbars more often than expected based on availability and selected natural and natural/modified habitats less than expected based on availability. DSR on engineered habitats was significantly higher than on natural or natural modified habitats (log odds: 2.71, 95% CI: 1.20 – 6.08). Thus, plovers' nest site selection may have increased their fitness. Predator exclosures around nests did not affect DSR after controlling for the effects of date, nest age, and the number of eggs. Our results suggest that habitat augmentation may stave off declines in piping plover populations limited by insufficient habitat and low nesting success.

KEY WORDS *Charadrius melodus*, habitat creation, Missouri River, nest exclosures, nest success, piping plover, shorebird.

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¹ E-mail: dcatlin@vt.edu

Understanding the factors that affect nest-site selection and nest survival is requisite for comprehending the population dynamics of imperiled birds and for implementing conservation strategies for those species (Martin 1993, Chalfoun and Martin 2007, Clark and Martin 2007). Loss and alteration of nesting habitat has contributed to the decline in nesting success through the loss of quality habitat and the increase in predation associated with marginal habitats (Tewksbury et al. 2006). The primary cause of nest failure for many shorebirds is predation (Prindiville Gaines and Ryan 1988, Rimmer and Deblinger 1990, Mayer and Ryan, 1991a, Melvin et al. 1992, Dowding and Murphy 2001, USFWS 2003, Conway et al. 2005, Ivan and Murphy 2005, Boettcher et al. 2007, Isaksson et al. 2007, Smith et al. 2007), but weather and flooding also may affect productivity (Espie et al. 1998, Conway et al. 2005).

Predator control, fences around nests to exclude predators (nest exclosures), and electric fencing have been used to increase reproductive output for shorebirds. Although in many studies exclosures increased hatching and reproductive output (Rimmer and Deblinger 1990, Melvin et al. 1992, Mayer and Ryan 1991a, Estelle et al. 1996, Johnson and Oring 2002, Murphy et al. 2003a, Neuman et al. 2004, Niehaus et al. 2004, Boettcher et al. 2007, Ivan and Murphy 2005, Isaksson et al. 2007), in other instances they were ineffective (Mabee and Estelle 2000). Exclosures often are most effective against predation from medium-sized mammals and birds such as coyotes (*Canis latrans*) and crows (*Corvus* sp.), but less so against small animals such as snakes and rodents (Mabee and Estelle 2000). Exclosures, however, can increase predation of adults if adults are less able to escape from these structures (Johnson and Oring 2002, Murphy et al. 2003b, Neuman et al. 2004, Niehaus et al. 2004, Boettcher et al. 2007, Isaksson et al. 2007). Several methods have been used to reduce such adult mortality (Murphy et al. 2003b), but the net effects of exclosures need to be evaluated on a case-by-case basis (Johnson and Oring 2002). Exclosures may not be a long-term solution to predation problems in some cases because of increased adult mortality, predator adaptation, or cost (Johnson and Oring 2002, Larson et al. 2003).

The negative effects of predation on populations through reduced productivity often are a symptom of other problems such as habitat loss or degradation (Yasué et al. 2007), increased human population, or introduced species (Dowding and Murphy 2001). Short-term measures such as predator control or exclusion may stop or reverse population declines temporarily, but these gains may be insignificant without long-term solutions (Johnson and Oring 2002). Habitat

creation or modification may be a necessary solution to the issue of declining habitat for some populations. For example, coastal dredge material disposal sites and other human-created habitats are known to support several species (Krogh and Schweitzer 1999, Mallach and Leberg 1999, Collis et al. 2001, Erwin et al. 2003, Spear et al. 2007, Yasué et al. 2007, Jenniges and Plettner 2008).

When evaluating the effect of habitat alterations or other management interventions on a population, managers should evaluate the overall fitness consequences of these actions. For example, high use of an engineered habitat may be counterproductive if the habitat is an ecological trap in which colonizing animals suffer reduced fitness due to low reproductive output or survival (Gates and Gysel 1978, Weldon and Haddad 2005). If there are new stresses (such as increased predation) in these habitats which would not have been experienced historically, then populations would be unable to appropriately evaluate the potential success within a habitat. For managed or created habitat to prove an effective conservation tool, it must both be selected for by the species of interest and provide at least comparable fitness relative to the habitat that it is replacing or augmenting.

Piping plovers (*Charadrius melodus*) on the Missouri River nest on sparsely vegetated sandbars, sandbar complexes (two or more adjacent sandbars separated by usually shallow streams of water), and lakeshores (Prindiville Gaines and Ryan 1988, Espie et al. 1996). These sandbars are created naturally when river flows transport and deposit sand. Decreased flows caused by dams on the mainstem of the river, however, have decreased the creation of new sandbar habitat, and the amount of existing habitat has been reduced by erosion and vegetation encroachment (USFWS 2003).

Predation of nests and chicks also has contributed to declines of this species (USFWS 2003), which is listed as threatened or endangered throughout its range in the United States and Canada. Proximity to vegetation is positively correlated with nest depredation (Espie et al. 1996). U.S. Army Corps of Engineers (USACE) management aimed at increasing productivity on Missouri River sites includes predator control, symbolic fencing (single strand of twine), habitat creation and modification, and erection of nest exclosures. We studied the effects of nest exclosures, habitat modification, and habitat creation by observing plover nest site selection and by comparing the success of plovers nesting on sandbars with various combinations of these treatments.

STUDY AREA

We studied piping plovers on 16 sandbar complexes on the Missouri National Recreational River below the Gavins Point Dam (42° 51' 43" N, 97° 29' 07" W; ca. 95 km of river) in 2005-2007. The Gavins Reach below the dam (hereafter Gavins) is one of the last free-flowing, unchannelized portions of the Missouri River, and piping plover habitat consists of sandbars that are largely unconnected to the shore. Much of the habitat available for nesting piping plovers resulted from sand deposited in relatively high flows during the 1990s. Existing sandbar habitat varies widely in size and composition, from low unvegetated mud and sandflats to high sandbars with cottonwood (*Populus* sp.) and willow (*Salix* sp.) saplings as the predominant vegetation type (LeFer 2005). Through the breeding season, herbaceous plants grow along the shorelines of most sandbars (LeFer 2005). In 2004, three sandbar complexes were created to augment current habitat. The USACE created these sandbars through a mixture of dredging and other mechanical methods (such as moving sediment with a bulldozer). In general, the engineered sandbars were longer than wide (in the direction of river flow), and in 2005, the three sandbars were 6.78, 20.58, and 20.71 ha each. In 2007, we included a newly engineered sandbar complex on Lewis and Clark Lake (hereafter the Lake). The Lake is a reservoir impounded by the Gavins Point Dam, and the sandbar complex was created within the upper portion of the Lake. The 2 sandbars in this complex were less elongate than those built in the river and encompassed 27.3 ha total during the 2007 breeding season.

In addition to sandbar creation, the USACE also modified natural habitat. They sprayed herbicide and cut vegetation on several sandbars within Gavins during the study. Contractors sprayed the vegetation (typically in early fall or late winter), and they used a brush-axe to mow down the vegetation (229.1 and 287.9 ha were sprayed and mowed respectively between 2005 and 2007). The USACE often did not remove the cut vegetation, so modified natural habitats often were a mixture of open dry sand patches and areas where cut vegetation and short stems were the primary ground cover. Natural modified habitats, however, varied widely in their treatments and appearance from year to year. The USACE only sprayed some sandbars without removing the vegetation, removing partial vegetation and burning the refuse in brush piles, and ultimately, many of the natural modified sandbars became densely vegetated by herbaceous plants (D. Catlin, personal observation). Of the 16 complexes in the study, 3 were modified in some way in 2005, and 3 sandbars were modified in 2006.

The primary cause of nest loss in our study appeared to be predation, but nests also were lost to flooding, bank erosion, abandonment, and trampling by various species. Potential nest predators in this region were coyotes, raccoon (*Procyon lotor*), American mink (*Mustela vison*), and American crow (*Corvus brachyrhynchos*).

METHODS

Field Techniques

Throughout the nesting season (April – July), we searched each sandbar by walking transects through potential piping plover nesting habitat. We used adult behavior as an indication of nesting. After a bird was observed that may have flushed from a nest, we crouched or hid nearby waiting for the bird to resume incubation. When a nest was found, we recorded its location using a handheld GPS unit (Trimble Geo-XT, Trimble Navigation, Ltd., Sunnyvale, CA). Except in 2005, at least one egg from all nests was floated at the time of discovery to determine the incubation stage and the timing of nest initiation (USACE, unpublished data). In 2005, eggs were floated if nests were found with 3 or 4 eggs. We visited nests approximately every other day until failure or hatching.

Analytical Methods

Phenology.— We divided the nesting season into 2-week periods, beginning with the first week that plover nests were initiated in the study (April 20th), and we used a χ^2 test for equal proportions to test for differences among years in the timing of initiation and hatching within these periods. Partial χ^2 values were used to further evaluate the results and to compare distributions among years.

Habitat Selection.— We calculated known habitat availability using land classification coverages collected during the 2005 – 2007 breeding seasons (L. Strong, US Geological Survey, unpublished data). Pan-sharpened multispectral QuickBird imagery was collected each year (between April and October) and classified using Definens Developer Software for a concurrent study of least tern (*Sternula antillarum*) and piping plover sandbar habitat availability (L. Strong, unpublished data). The amount of suitable habitat was calculated as the amount of open and sparsely vegetated wet and dry sand habitat on a sandbar. Use was estimated from the number of nests initiated in a given habitat type within a year. For the use vs. availability analysis, we used a χ^2 test to determine overall selection within each of the years and compared 95% CIs of proportion of use to known availability to determine selection for or against a particular sandbar

type: natural, modified natural, and engineered (Neu et al. 1974, Byers and Steinhorst 1984). We compared habitat selection among years to describe changes in selection over time.

Nesting Success.— We considered a nest that hatched ≥ 1 chick to be successful. For nests where chicks were never seen, we considered a nest “possibly successful” if one or more eggs disappeared with no sign of predation within ± 2 days of the estimated hatch date (34 days from nest initiation, Elliot-Smith and Haig 2004). For the analysis, we censored possibly successful nests at the time of last known activity. We determined the failure date for abandoned nests by examining visit records and using information regarding the presence or absence of adults.

We used a random effects logistic-exposure model (Rotella et al. 2004, Shaffer 2004, Stephens et al. 2005) to estimate the daily survival rate (DSR) of nests in our study. The logistic exposure model is a generalized linear model that uses a logit link to relate DSR to the regression:

$$DSR_i = \frac{e^{\beta_0 + \sum_j \beta_j x_{ji}}}{1 + e^{\beta_0 + \sum_j \beta_j x_{ji}}}$$

where i represents day, j the covariates, and β_j the coefficient of covariate j (Rotella et al. 2004). By exponentiating the individual β estimates, we produced log-odds ratios that represent multiplicative change in DSR associated with each covariate.

We developed several a priori hypotheses for the factors that affect nesting success:

1. Nest Exclosures: The exclosing of nests is a common management practice for piping plovers and other shorebirds and has been shown to significantly increase daily survival rate (Rimmer and Deblinger 1990, Mayer and Ryan 1991a, Melvin et al. 1992, Estelle et al. 1996, Johnson and Oring 2002, Murphy et al. 2003a, Neuman et al. 2004, Niehaus et al. 2004, Boettcher et al. 2007, Ivan and Murphy 2005, Isaksson et al. 2007, Cohen et al. in press). We hypothesized that exclosures would increase nest survival.
2. Sandbar Type: We hypothesized that nests on engineered sandbars would have higher nest success than those on natural sandbars. We believed these sandbars would be less susceptible to predation since they had little to no cover in which predators could hide and because they represented new areas not discovered by predators (Prindiville Gaines and Ryan 1988, Espie et al. 1996). In addition, we hypothesized that nests on modified natural sandbars also would have higher nest

- success than those on natural sandbars because of the reduction in vegetation (Espie et al. 1996).
3. Nest Age: Nest survival may vary according to nest age (Klett and Johnson 1982, Johnson and Walters 2008). We hypothesized that older nests would have a greater daily survival than younger nests. If nests that are poorly concealed or otherwise at higher risk fail soon after initiation, then DSR ought to increase with increasing nest age (Klett and Johnson 1982). In addition, we examined possible non-linearity in this effect by adding quadratic terms to some models.
 4. Number of eggs: We hypothesized that the number of eggs within a clutch would be positively related to DSR. As the number of eggs within a clutch increases, so does incubation length in piping plovers (Elliot-Smith and Haig 2004, Catlin and Fraser, unpublished data). Nests with more eggs could benefit from reduced activity at the nest site and from increasing parental camouflage from the incubating adult.
 5. Nest Density: We hypothesized that nesting success would decrease with increasing nesting density (Gunnarson and Elmberg 2008). We used this variable to explore negative density-dependent effects on nesting success.
 6. Date: We hypothesized that nest survival would increase throughout the breeding season because of the presence of least tern (*Sternula antillarum*) colonies later in the season because least terns actively defend their colonies by mobbing intruders (Burger 1987, Paulson and Erckmann 1985, Lauro and Tanacredi 2002, Nguyen et al. 2003) or potentially through a dilution effect. We also examined the potential for non-linearity in this effect by adding a quadratic effect of date.
 7. Exclosure Interactions: We hypothesized that the positive effect of exclosures on nest success could mask the other effects that we modeled, so we tested interactions between exclosures and age (linear only), date (linear only), number of eggs, nest density, and sandbar type.
 8. Random effect: Controlling for the dependence of nest fates is an important issue for nest survival studies (Stephens et al. 2005). We included a random effect for a sandbar*year interaction in all of our models under the assumption that the fates of nests on the same sandbar in the same year may not be independent of one another.

We tested fit of the global model (includes all of the variables) with a Hosmer and Lemeshow goodness of fit test (Hosmer and Lemeshow 1989, Shaffer 2004). We examined all possible subset models of the above variables (Montgomery et al. 2001). These models were analyzed using Proc NLMIXED (SAS Institute, 2004), and we used Akaike's Information Criterion, corrected for small sample size (AIC_c) to rank models (Burnham and Anderson 2002). In addition, we used the Akaike's weights to create model-averaged parameter estimates, unconditional standard errors, and a relative importance index for variables (RI; Burnham and Anderson 2002). We used the model-averaged parameter estimates to evaluate our hypotheses about DSR. In particular, we used the RIs and the coverage of 95% confidence intervals for the beta estimates for each of the variables in our all possible subsets models to determine the importance of each of the variables.

RESULTS

Phenology

We monitored 623 piping plover nests from 2005 – 2007. Sample sizes for each of the analyses varied as a result of incomplete information in some cases. Nest initiation began in late April and was highest in May and early June (Fig. 1a). Initiation dates differed by year ($\chi^2_{10} = 50.49$, $P < 0.0001$, $n = 608$) and were earlier in 2007. Fewer nests were initiated in late April and early May in 2005 (Partial $\chi^2 = 5.41$ and 5.22 , respectively) and more were initiated in late April in 2007 (Partial $\chi^2 = 11.41$; Fig. 1a) than in other years. Initiation dates differed by sandbar type ($\chi^2_{10} = 19.98$, $P = 0.029$, $n = 608$). More nests were initiated in late April on natural sandbars (Partial $\chi^2 = 4.97$) than on the other two sandbar types.

Hatching began in late May and early June and was greatest in June and early July (Fig. 1b). Hatching date differed by year ($\chi^2_{10} = 33.16$, $P = 0.0003$, $n = 352$). Hatching dates were later in 2005 than in other years (Partial $\chi^2 = 5.77$, for 15 Jul to 29 Jul 2005; Fig. 1b). Hatching dates differed by sandbar type ($\chi^2_{10} = 18.70$, $P = 0.044$, $n = 352$). There were more hatches on modified natural sandbars in late May than on the other types of sandbar (Partial $\chi^2 = 7.66$)

Habitat Selection

Piping plovers used all habitat types in proportion to their availability in 2005 (Table 1). In 2006 and 2007 they used engineered sandbars more and modified and natural sandbars less than expected based on availability (Table 1).

Nest Survival

Raw success rates remained relatively stable throughout the study (mean visit interval from 2005 – 2007 = 2.19 ± 0.01 days, $\bar{x} \pm 1SE$; Table 2). Sandbar type, nest exclosures, date, nest age, and the number of eggs were the most important variables affecting nest survival ($RI > 0.90$; Table 3). Nests on engineered sandbars had a 2.5-fold higher DSR than those on natural sandbars (Table 3, Fig. 2), but nests on modified/natural sandbars showed no difference (95% CI overlapped 0, Table 3, Fig. 2). The presence of nest exclosures, however, had a positive but insignificant effect on DSR (Table 3). DSR increased through the season by a factor of 1.05 d^{-1} past 20 April of each year (Table 3, Figs. 2,3). In contrast, as nest age increased DSR decreased by a factor of 0.90 d^{-1} (Table 3). DSR increased by a factor of 1.63 egg^{-1} (Table 3, Fig. 3). None of the other factors that we tested significantly affected DSR (Table 3).

DISCUSSION

Our results suggest that piping plovers perceived engineered habitat to be a suitable nesting substrate. While piping plovers selected for engineered sandbars and increased their nesting success in doing so, they simultaneously selected against modified natural habitat, but nesting success was not different between natural and modified natural sandbars. The newly created habitat was similar to natural habitats used by piping plovers, *viz.* open dry sand and pebbles with sparse vegetation (Elliot-Smith and Haig 2004). Similar to the engineered habitat in this study, dredge spoil islands in coastal habitats have been used by several species (Krogh and Schweitzer 1999, Mallach and Leberg 1999, Collis et al. 2001, Erwin et al. 2003, Spear et al. 2007), showing the potential for replacement or augmentation of natural habitat that is unavailable or otherwise degraded. This study, however, reflects only the first 3 – 4 years following the creation of this habitat; it does not speak to the long-term effects of this type of habitat on piping plover population dynamics.

Overall, daily survival rates for piping plover nests in this study (95% CI: 0.978 – 0.979) were comparable to those for piping plovers elsewhere (range: 0.93 – 0.99; Prindiville Gaines and Ryan 1988, Patterson et al. 1991, Melvin et al. 1992, Mabee and Estelle 2000, Cohen 2005, Harris et al. 2005, Houghton 2005, Ivan and Murphy 2005), suggesting that the general limitations to nesting success on the Missouri River are similar to those elsewhere in the range, despite the fact that the specific threats may be different.

There was no evidence that the specific modifications of habitat between 2005 and 2007 increased or decreased nest survival, but selection against this habitat brings its usefulness into question. The maintenance of dredge spoil islands has been proposed as a means for improving productivity of waterbirds using these sites (Erwin et al. 2003, Spear et al. 2007), but recent efforts to improve natural habitat on the Missouri River have failed, resulting in selection against these habitats and no increase in nesting success. The methods used, however, are still in the development stage, and habitat modification may yet provide suitable nesting habitat for piping plovers on the Missouri River. Additionally, the habitat modification project coincided with several low-water years that exposed normally inundated sandbars (G. Jons, USACE, personal communication). It is possible that at normal water flows, when these low-lying sandbars are inundated, or with a more complete removal of vegetation that plovers would select for the modified natural habitat.

The lowest nest DSRs occurred in the beginning of the breeding season and DSR increased with increasing date, which may have been related to the timing of the endangered least tern (*Sternula antillarum*) nesting. Piping plovers and other shorebirds may benefit from nesting within colonies of birds that practice aggressive defense against depredation (Paulson and Erckmann 1985, Burger 1987, Lauro and Tanacredi 2002, Nguyen et al. 2003), but in some instances they do not (Mayer and Ryan 1991b). For example, Lauro and Tanacredi (2002) found that artificial piping plover nests had greater survival within common tern (*Sterna hirundo*) colonies than in other habitats, but a study of artificial plover nests among American avocet (*Recurvirostra americana*) colonies showed no benefit to nesting within the avocet colony (Mayer and Ryan 1991b). The USACE's habitat creation project also was concerned with recovery of the endangered interior least tern, and this dual purpose may serve to further benefit piping plover recovery, assuming that nesting among least terns confers some added protection to piping plovers.

Nest predators in other systems have shown prey switching behavior in response to changing prey availability (Abrams and Matsuda 1996, Lecomte et al. 2008, Norbury and Heyward 2008), and it is possible that increased DSRs later in the season were a result of predators such as crows, coyotes, and raccoons finding alternative prey. Again, the timing of least tern nesting could be a contributing factor to piping plover nest survival later in the season since their initiation dates are considerably later on average than those for piping plovers (mean

initiation dates from 2005 – 2007 were in the first and second weeks in June, [Mark Sherfy, USGS, personal communication]) which could reduce predation on piping plover nests (Abrams and Matsuda 1996). Further study of the food habits of the common nest predators on the Missouri River is needed to determine whether such a pattern is occurring.

As we had hypothesized, DSR was positively related to the number of eggs within a clutch regardless of nest age. This increase in DSR with the number of eggs may reflect differing behavioral patterns near the nest as the number of eggs increases. The time spent daily in incubation increases with the number of eggs within a piping plover nest (Elliot-Smith and Haig 2004), and nests may benefit from the increased camouflage of an incubating adult or the reduced activity at nests associated with longer bouts of incubation. The relationship between DSR and the number of eggs may also reflect the effects of partial clutch loss from depredation or weather leading to total clutch loss or an increased potential for abandonment. Partial clutch loss is followed by increased incidence of abandonment in waterfowl (Armstrong and Robertson 1988). If the potential gains from continuing to incubate a partial clutch are not greater than those from abandonment and attempting to breed again within the same season or abandonment and waiting until the next season, then piping plovers ought to abandon partial clutches, regardless of clutch size.

Contrary to our hypothesis, as nest age increased, DSR decreased after accounting for the number of eggs. We hypothesized that the failure of the most easily detected nests would decrease DSR at early nest ages (Klett and Johnson 1982), but the pattern of age-dependent nest failure observed did not support this hypothesis. Johnson and Walters (2008) found a similar pattern of declining success with nest age in western sandpipers (*Calidris mauri*), but they found that this pattern was strongest in first- and second-year breeders. They hypothesized that the increasing demands of incubation at later nest ages may have prohibited inexperienced breeders from fully caring for their nests (Johnson and Walters 2008). We did not know the breeding experience of the adults at most of our nests, but continued sampling could provide the necessary data to examine this hypothesis. It is possible that delayed departure of adults at nests that were eventually abandoned could have affected this parameter estimate; 17% of all failures were attributed to abandonment (Table 2). Defining a time of failure for an abandoned nest is difficult given the many possibilities for the abandonment and the proximate cause of failure. Alternatively, if our window for defining a probable hatch (± 2 days from the expected hatch

date) precluded some successful nests, our estimate of DSR for older nests could be biased low. However, only 3 nests were deemed failed because of a total loss of the clutch between 2 – 5 days before the expected hatch date, suggesting that our window was not producing this nest age effect.

Although the effect of nest exclosures was statistically non-significant, the large point estimate and RI value suggest that exclosures could have a positive effect on nesting success. Several studies have demonstrated increased productivity associated with the use of fences and exclosures on shorebird nests, with exclosure treatments improving raw and Mayfield DSR estimates by an order of 1.02 – 1.87 (Rimmer and Deblinger 1990, Mayer and Ryan 1991a, Melvin et al. 1992, Estelle et al. 1996, Johnson and Oring 2002, Murphy et al. 2003a, Neuman et al. 2004, Niehaus et al. 2004, Houghton 2005, Ivan and Murphy 2005, Isaksson et al. 2007). Similar to our study, Mabee and Estelle (2000), however, found no effect of exclosures on three shorebird species: piping plover, snowy plover (*Charadrius alexandrinus*), and killdeer (*C. vociferus*). The authors attributed the lack of effect to differences in predator communities and to a lack of statistical rigor in previous studies leading to bias in estimates of DSR and nesting success (Mabee and Estelle 2000). The predator community in the Mabee and Estelle (2000) study was comprised of smaller animals (snakes and rodents) that were not deterred by the cages, but most of the animals that are frequent nest predators on the Gavins Reach and Lewis and Clark Lake were medium- to large-sized mammals (coyotes, raccoons) and birds (crows) that could be effectively deterred by exclosures. Our study did however suffer in that the placement of exclosures was not random and there were not equal sample sizes of exclosed and unexclosed nests through time or through space. The USACE monitoring crew was responsible for the exclosing of nests and their monitoring season began after the initiation of the breeding season, nests were not exclosed until clutches were completed, and areas of higher nesting density tended to receive greater management attention (D. Catlin, pers. obs.).

Although exclosures may have a positive effect on the productivity of shorebirds, they also have been associated with an increasing predation risk to adult birds (Johnson and Oring 2002, Murphy et al. 2003b, Neuman et al. 2004, Isaksson et al. 2007), which could lead to nest abandonments and an overall reduction in reproductive output. Adult shorebirds within exclosures have been killed by mammalian (Johnson and Oring, 2002) and avian (Murphy et al. 2003b, Neuman et al. 2004) predators. We found feather piles and other signs of predation with

great-horned owl (*Bubo virginianus*) and mink tracks at some exclosed nests. In addition, remote-camera photographs of great-horned owls perching on top of active nests with exclosures were taken during the 2008 breeding season (J. Felio et al., unpublished data). Murphy et al. (2003b) found that smaller exclosures and the use of exclosures near forest cover were associated with higher percentages of adult mortalities. The corridor of the Missouri River on the Gavins Point Reach and Lewis and Clark Lake is largely forested and the exclosures used are relatively small for portability to sandbars, which could contribute to adult mortality at nest exclosures. Johnson and Oring (2002) suggested that exclosures should only be used as short-term solutions until long-term conservation can be implemented. Despite potential increases in productivity associated with exclosures, the mortalities and owl activity confirm that other solutions are necessary.

MANAGEMENT RECOMMENDATIONS

The habitat creation program may offer solutions to reduced habitat availability and nesting success for the piping plover on the Missouri River. Plovers began selecting for engineered habitat soon after its creation, suggesting that in times of high reproductive success, these sites could be important for recruitment, and ultimately population growth. By creating habitat to recruit these new birds into the population, we could make greater strides toward recovery than without such habitat. In addition, nesting success was higher on engineered habitat than on natural or modified habitat, indicating that the habitat creation program provided high quality nesting habitat. Although we did not find a significant effect of exclosures, we do not suggest the practice be abandoned on the Missouri River or elsewhere, particularly given the high RI value (0.99) and point estimate (17.99) associated with the presence of exclosures. With intensive monitoring and management, exclosures can be deployed in an area with specific predator issues quickly and efficiently, but where monitoring is less frequent, broad application of exclosures could alleviate acute predation issues. The potential benefits, however, need to be weighed against the potential for adult mortality.

Habitat selection and nesting success are only two metrics by which engineered sandbars need to be measured. Ultimately, the effects of these actions on population growth will be the most important metric. Our results show that piping plover populations can benefit from the use of created habitat, but these results will need to be coupled with studies of the effects on other

measures of productivity, such as chick survival and recruitment, and ultimately on population growth.

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Figure 1: Piping plover nest initiation (A) and hatching (B) dates from 2005 – 2007 for the Gavins Point Reach and Lewis and Clark Lake on the Missouri River.

Figure 2: Estimated daily survival rate by sandbar type (natural and engineered) for piping plover nests on the Gavins Point Reach and Lewis and Clark Lake on the Missouri River plotted by date. Values were calculated using the model-averaged parameter estimates from all variables. Values for all variables other than date and sandbar type were held constant at the sample average.

Figure 3: Estimated daily survival rate by egg number (1 – 4 eggs) for piping plover nests on the Gavins Point Reach and Lewis and Clark Lake on the Missouri River plotted by date. Values were calculated using the model-averaged parameter estimates from all variables. Values for all variables other than date and egg number were held constant at the sample average.

Table 1: Use vs. availability of sandbar habitat for piping plover nesting on the Missouri River during the 2005 – 2007 field seasons with respect to habitat modifications. Use was defined as the number of nests that were initiated on each type of habitat within each year. Subscripts on the proportion of available habitat represent selection (+ selection for, - selection against, and = no selection).

Year ^a	Natural Sandbars			Modified Natural Sandbars			Engineered Sandbars		
	<i>n</i> ^b	Pu _i (95% CI) ^c	Pa _i ^d	<i>n</i>	Pu _i (95% CI)	Pa _i	<i>n</i>	Pu _i (95% CI)	Pa _i
2005	87	0.431 (0.348, 0.514)	0.510 =	42	0.208 (0.140, 0.276)	0.193 =	73	0.361 (0.280, 0.442)	0.297 =
2006*	48	0.232 (0.162, 0.302)	0.500 .	31	0.150 (0.091, 0.209)	0.275 .	128	0.618 (0.537, 0.699)	0.224 +
2007*	54	0.252 (0.181, 0.323)	0.384 .	18	0.084 (0.039, 0.129)	0.161 .	142	0.664 (0.587, 0.741)	0.455 +

^a Years that showed statistically significant overall selection for or against certain sandbar types from the χ^2 goodness of fit test ($P < 0.05$) are marked with an asterisk (2005: $\chi^2 = 2.15$, $P = 0.341$; 2006: $\chi^2 = 50.32$, $P < 0.001$; 2007: $\chi^2 = 14.28$, $P < 0.001$).

^b Number of nests initiated on each habitat type within each year.

^c Proportion of use (Pu) for each year in each of the sandbar classes for each year, as determined from aerial photography and land cover classification.

^d Proportion of nesting habitat available (Pa) in each of the sandbar classes for each year, as determined from aerial photography and land cover classification.

Table 2: Raw nest success (% total) for piping plover nests on the Missouri River during the 2005 – 2007 nesting seasons. Known successful nests had one or more chicks associated with the nest or the parents of the nest. Possibly successful nests did not have chicks associated with the nest or adults but eggs disappeared within 2 days of the projected hatch date. Failed nests did not have chicks associated with the nest or adults and disappeared outside the window of reasonable hatch dates (excluding abandoned nests).

Year	Total Nests	Known Successful	Possibly Successful	Failed Predation	Failed Abandoned	Failed Flooding	Failed Other ^a	Failed Unknown
2005	183	97 (53.0%)	12 (6.6%)	18 (9.8%)	7 (3.8%)	1 (0.5%)	5 (2.7%)	43 (23.5%)
2006	205	105 (51.2%)	6 (2.9%)	17 (8.3%)	21 (10.2%)	10 (4.9%)	4 (2.0%)	42 (20.5%)
2007 ^b	211	107 (50.7%)	18 (8.5%)	48 (22.7%)	15 (7.1%)	9 (4.3%)	2 (0.9%)	12 (5.7%)
Total	599	309 (51.6%)	36 (6.0%)	83 (13.9%)	43 (7.2%)	20 (3.3%)	11 (1.8%)	97 (16.2%)

^a Includes bank erosion, weather events, and nests stepped on by researchers.

^b Change in protocols led to more failures classified as predation. If eggs were missing before the hatch date and none of the other causes of failure were implicated, predation was thought the likely cause. The other frequent causes of nest loss, abandonment and flooding were obvious to observers. Many of the unknown nest losses from 2005 and 2006 were probably as a result of predation.

Table 3: Model-averaged parameter estimates, unconditional standard errors, and 95% confidence intervals from an all possible subsets regression (Montgomery et al. 2001) for parameters affecting daily survival rate of piping plovers nesting on the Gavins Point Reach and Lewis and Clark Lake on the Missouri River, during the 2005 – 2007 nesting seasons.

Variable	Parameter Estimate ^a	Uncond. SE ^b	95% CI LL,UL	Log-odds Ratio	95% CI Log-odds LL, UL	RI ^c
Intercept	0.893	0.517	−0.120, 1.906	NA	NA	1.000
Exclosing ^d	2.890	1.715	−0.471, 6.251	17.991	0.624, 518.6	0.997
Nest Age	−0.104	0.050	−0.203, −0.005	0.901	0.817, 0.995	0.982
Nest Age ²	0.003	0.002	−3E−4, 0.006	1.003	1.000, 1.006	0.877
Date	0.044	0.021	0.002, 0.085	1.045	1.002, 1.089	1.000
Date ²	−2E−4	−2E−4	−0.001, 3E−4	1.000	0.999, 1.000	0.511
Number of Eggs ^e	0.488	0.095	0.302, 0.675	1.630	1.352, 1.964	1.000
Nest Density ^f	−0.092	0.139	−0.364, 0.179	0.912	0.695, 1.196	0.730
Nest Number ^g	0.001	0.003	−0.006, 0.007	1.001	0.994, 1.008	0.175
Exclosure Number ^h	0.023	0.040	−0.055, 0.102	1.023	0.946, 1.107	0.175
Nest * Exclosure Number ⁱ	−0.001	0.001	−0.002, 0.001	0.999	0.998, 1.001	0.175
Engineered Sandbar	0.917	0.442	0.051, 1.782	2.501	1.052, 5.943	0.933
Modified Sandbar	−0.194	0.350	−0.880, 0.492	0.824	0.415, 1.635	0.933
Exclosure*Age	−0.064	0.042	−0.146, 0.018	0.938	0.865, 1.018	0.832
Exclosure*Date	0.002	0.008	−0.013, 0.018	1.002	0.987, 1.018	0.331
Exclosure*Number of Eggs	−0.380	0.313	−0.992, 0.233	0.684	0.371, 1.262	0.760

Exclosure*Nest Density	0.517	0.408	−0.283, 1.317	1.678	0.754, 3.73	0.690
Exclosure*Engineered Sandbar	−0.833	0.700	−2.206, 0.539	0.435	0.110, 1.715	0.713
Exclosure*Modified Sandbar	0.456	0.727	−0.968, 1.880	1.578	0.380, 6.555	0.713
Random Effect	0.585	0.221	0.152, 1.017	NA	NA	1.000

^a Model-averaged parameter estimates (Burnham and Anderson 2002), averaged over all possible subset models.

^b Unconditional standard error (Burnham and Anderson 2002).

^c Relative importance of each of the variables. Equal to the sum of the AIC_c weights of each of the models including that variable (Burnham and Anderson 2002).

^d Nest exclosing refers to the placement of a protective metal cage around the nest to prevent predation.

^e Measured as the number of eggs at the beginning of an observation interval.

^f Average number of active nests on the sandbar within the observation interval per hectare of nesting habitat.

^g Average number of active nests on the sandbar within the observation interval.

^h Average number of exclosed nests on the sandbar within the observation interval.

ⁱ Interaction between the average number of nests and average number of exclosed nests on a sandbar within the observation interval.

Figure 1:

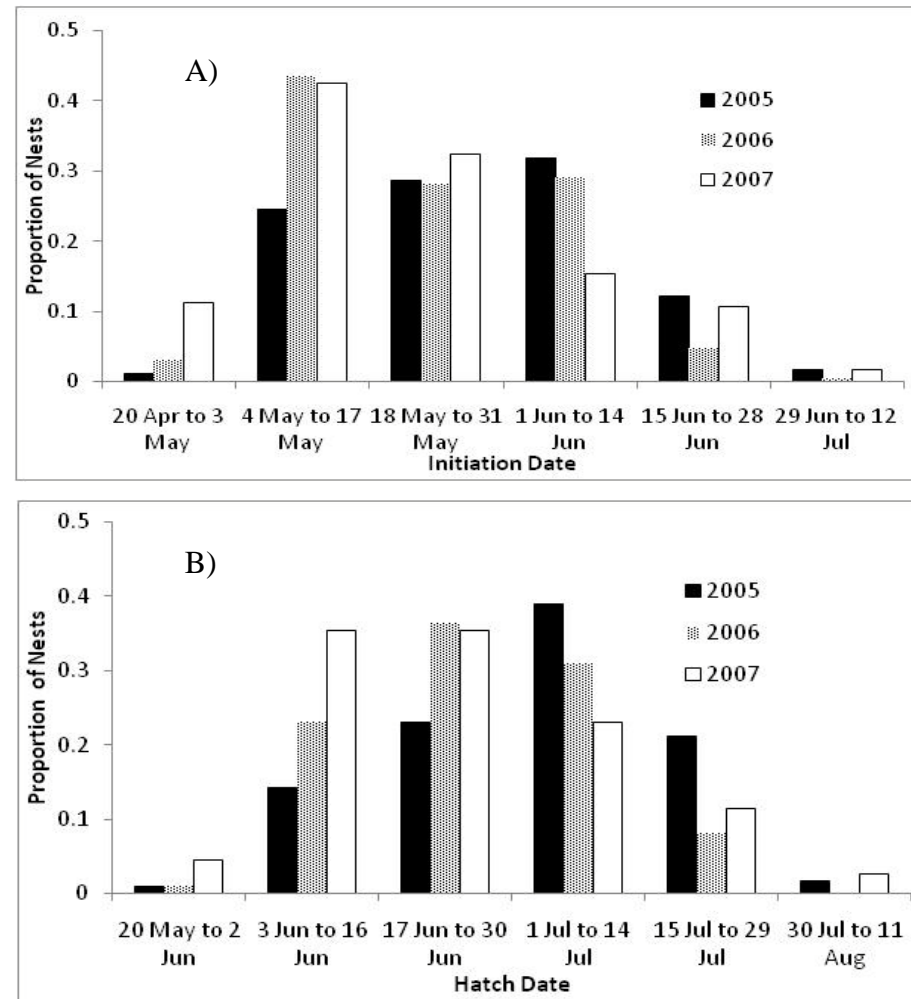


Figure 2:

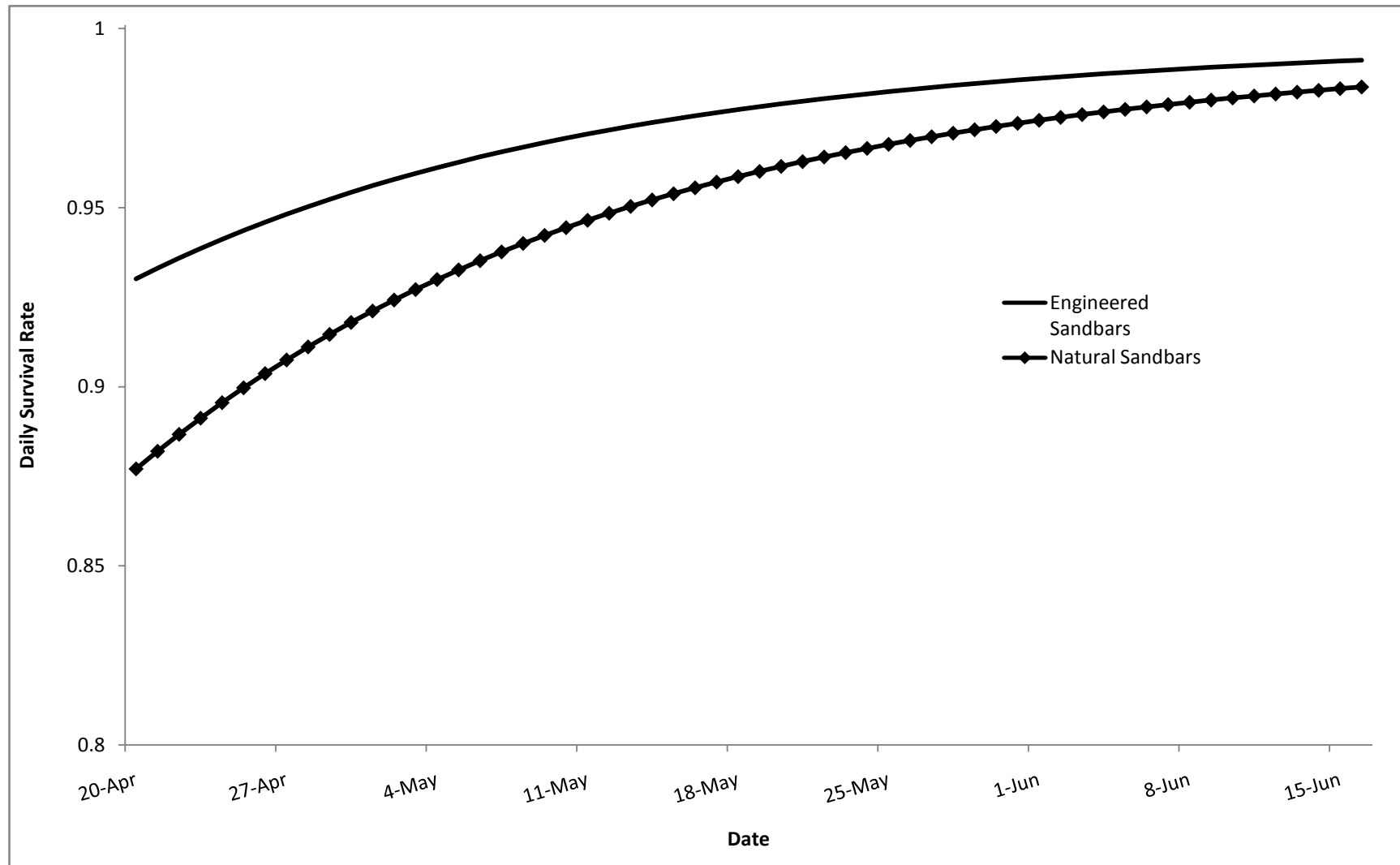
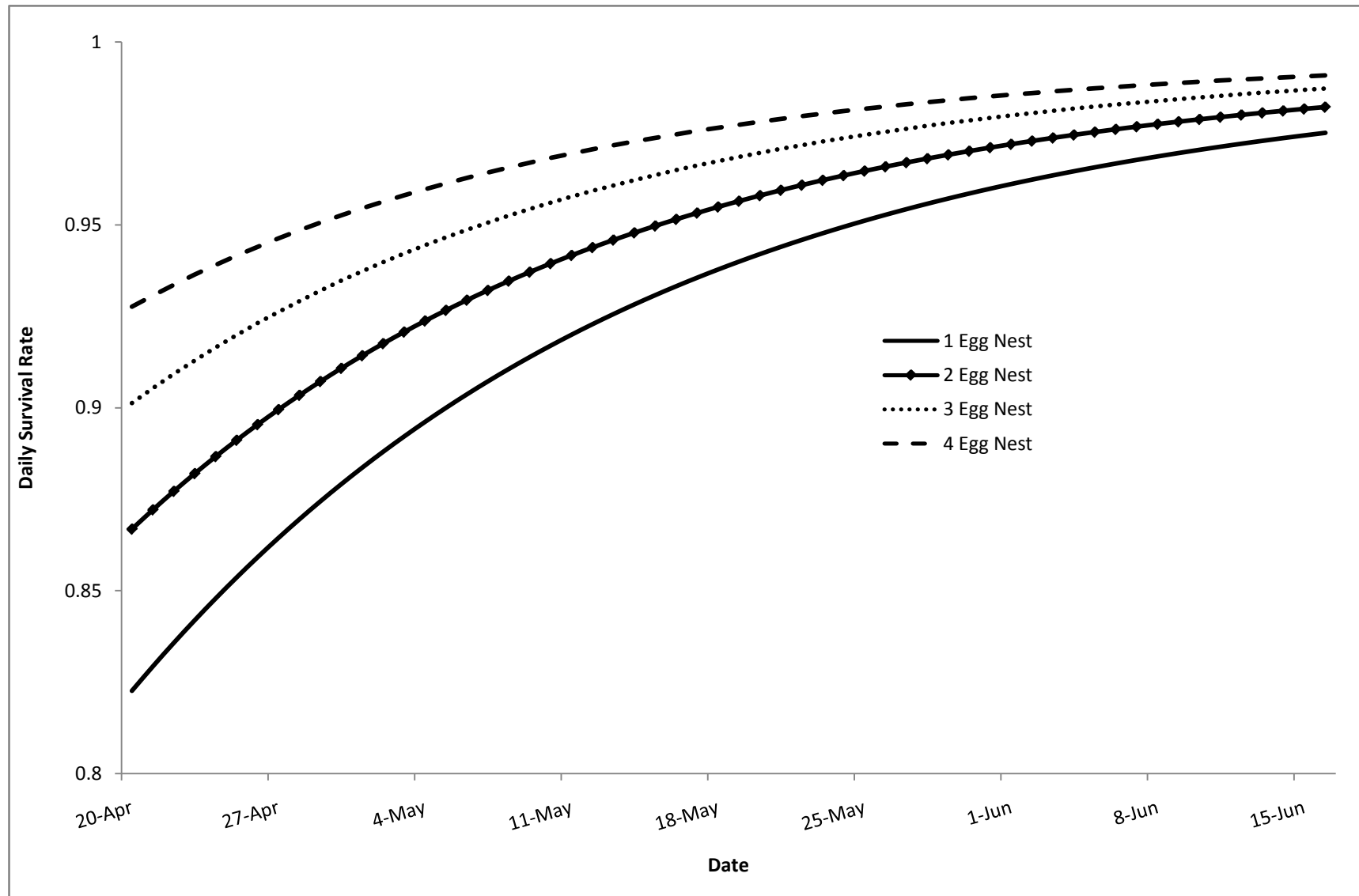


Figure 3:



Chapter 2: Density-Dependent Population Dynamics in Piping Plovers *Charadrius melodus*:
Consequences of a Conservation Experiment
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Density-Dependent Population Dynamics in Piping Plovers *Charadrius melodus*: Consequences of a Conservation Experiment

Daniel H. Catlin^a, Department of Fisheries and Wildlife Sciences, Virginia Polytechnic Institute and State University, Virginia.

James D. Fraser, Department of Fisheries and Wildlife Sciences, Virginia Polytechnic Institute and State University, Virginia.

Joy H. Felio, Department of Fisheries and Wildlife Sciences, Virginia Polytechnic Institute and State University, Virginia.

Jonathan B. Cohen, Department of Fisheries and Wildlife Sciences, Virginia Polytechnic Institute and State University, Virginia.

^a Corresponding author, Ph: 01-540-231-1692, Fax: 01-540-231-7580, email: dcatlin@vt.edu

Summary

1. Density-dependent effects on population dynamics can have profound consequences for conservation strategies. These effects, however, are rarely estimated because of the difficulty in obtaining them.
2. We used capture-mark-recapture methods to investigate the relationship between survival, movement, and density in an imperiled North American shorebird, the piping plover *Charadrius melodus*, in response to the experimental creation of sandbar habitat.
3. Juvenile survival was negatively related to nesting density on relatively densely populated, newly created sandbars, and positively related to density on the less dense, natural sandbars. We found no evidence of density-dependent adult survival within our study area.
4. Juveniles from densely-populated, engineered sandbars were more likely to breed on natural habitat the following year than those on less densely-populated sandbars, and, in general, movements of both juveniles and adults suggested a preference for engineered habitat by adults.
5. Emigration from the study area by adults and juveniles was highest in the second year of the study. This increase corresponded with an increase in overall density of the population, an increase in water discharge, and a decrease in reproductive success.
6. *Synthesis and application.* Our results indicate that density-dependent survival and movement are integral to conservation planning, and that when density-dependent effects

are occurring, habitat use can be a misleading metric for use in evaluation of habitat management.

Key-words: density dependence, endangered species, habitat creation, population regulation, survival, Missouri River

Introduction

The roles of survival, reproduction, immigration, and emigration in population regulation are well established both theoretically and empirically (Lack 1966, Murray 1994, Newton 1998, Hixon et al. 2002). Studies of survival can be particularly important in determining the causes of decline for species of conservation concern (Baillie 2001). The causes of avian mortality vary from species to species, but predation, starvation, disease, and anthropogenic effects seem to have the largest effect on survival (Newton 1998). Several studies have further found a link between survival and density, such that one or more of these causes of mortality are exacerbated at higher densities (Tinbergen et al. 1985, Wylie and Newton 1991, Newton 1998, Paradis et al. 2002, Tavecchia et al. 2007). Competition for food at high population densities can lead to increased starvation through decreased intake rates, either directly from depletion or indirectly through interference (Goss-Custard et al. 2001). Additionally, denser conglomerations of birds can suffer greater predation (Durrell 2000, Whitfield 2003a, Whitfield 2003b). While density-dependent effects on survival often are inferred from count data (Newton 1994, Newton 1998), few studies have directly investigated the links between density and survival parameters (Paradis et al. 2002). Far more effort has been expended on determining the relationships between productivity and density than between survival and density (Newton 1998), suggesting the need for further research in this area.

Beyond survival and productivity, populations may be regulated through immigration and emigration. Because these parameters can have profound effects on populations; ignoring them can obscure the nature of population dynamics (Hixon et al. 2002). Factors such as age, sex, and reproductive success often contribute to both the occurrence and magnitude of dispersal in birds (Greenwood and Harvey 1982). In many bird species, adult emigration is negatively related to individual reproductive success (Greenwood and Harvey 1982, Johnson and Gaines 1990, Wiklund 1996, Gowaty and Plissner 1997, Haas 1998, Catlin et al. 2005) as well as conspecific reproductive success (Danchin et al. 1998, Brown et al. 2000, Doligez et al. 2002, Hénau et al. 2007, Boulinier et al. 2008), and emigration is greater in young individuals, potentially as a

mechanism to avoid inbreeding (Greenwood and Harvey 1982, Johnson and Gaines 1990) or to avoid competition among kin (Bowler and Benton 2005). Like survival and reproduction, immigration and emigration can be affected by density (Lindberg et al. 1998, Matthysen 2005, Hénau et al. 2007, Tavecchia et al. 2007). Dispersing from high density areas may be a way for some birds to increase fitness particularly in heterogeneous habitats (Matthysen 2005). If density-dependent regulation exists in birds (Lack 1966, Newton 1998), then human-induced decreases in habitat quantity and quality are of particular concern to the conservation of imperiled species (Newton 1994). Elucidation of the prominent factors regulating population size is then essential to plans for conservation and recovery.

Piping plovers (*Charadrius melodus*) on the Missouri River nest on the ground, primarily on sparsely vegetated sandbars and lakeshores (Prindiville Gaines and Ryan 1988, Espie et al. 1996), and appear to be limited by habitat loss and degradation (USFWS 2003). Sandbars were deposited and vegetation was scoured by high flows before dams were installed on the mainstem of the Missouri River in the mid-20th century. Decreased flows caused by these dams, however, have decreased the creation of new sandbar habitat, and existing habitat has been lost or degraded through vegetation encroachment and become unavailable through continued erosion (USFWS 2003), leading to a decline in habitat quantity and quality for piping plovers. Predation of nests and chicks also has contributed to declines in this species, which is listed as threatened or endangered throughout its range in the United States (USFWS 2003).

The U.S. Army Corps of Engineers (USACE) management for increased piping plover reproductive output on the Missouri River includes symbolic fencing (stakes, twine, and informational signs near or around nesting sites to prevent disturbance by humans), nest exclosures (small cages to deter nest predators), predator control (trapping and removal), and habitat creation. We studied the survival and movement (both within the study area and emigration outside of the study area) of adult and juvenile piping plovers nesting on engineered and natural/modified sandbars on the Missouri River. The objectives of this study were to evaluate the effects of density on survival and movement and to compare engineered and natural habitat with respect to survival and movement.

Methods

STUDY AREA

We studied piping plovers on the stretch of the Missouri National Recreational River below the Gavins Point Dam (ca. 95 km of river) in 2005-2007, which included a newly created engineered sandbar on Lewis and Clark Lake (the Lake) in 2007. The Gavins Reach is one of the last free-flowing, unchannelized portions of the Missouri River, and piping plover habitat consists of sandbars that are largely unconnected from the shore. Much of the habitat available for nesting for piping plovers consisted of sand deposited during relatively high flows in the late 1990s (USFWS 2003). Existing natural sandbar habitat varies widely in size and composition, from low unvegetated mud and sandflats, to higher sandbars with stands of cottonwood (*Populus* sp.) and willow (*Salix* sp.) saplings (LeFer 2005). Through the breeding season, herbaceous plants grew along the shorelines of most sandbars (LeFer 2005). In 2004, three sandbar complexes (2 or more sandbars separated by relatively shallow channels) were created to augment current habitat. The USACE created these sandbars through a mixture of dredging and other mechanical methods (such as moving sediment with a bulldozer). In general, the engineered sandbars were longer than wide (in the direction of river flow), and in 2005, the three sandbars were 6.78, 20.58, and 20.71 ha, respectively. In 2007, a sandbar complex was created within the upper portion of the Lake (ca. 27 km from the Gavins Point Reach and ca. 37 km from the nearest river sandbar in this study), and this complex was added to the research area for this study. The 2 sandbars in this complex were less elongate than those built in the river and totaled 27.3 ha during the 2007 breeding season. The study included 12 natural sandbar complexes and 4 engineered sandbar complexes.

FIELD METHODS

Throughout the nesting season (April – July), we searched sandbars for nests, walking transects through potential piping plover nesting habitat. We recorded each nest location on a handheld GPS unit (Trimble Geo-XT, Trimble Navigation, Ltd., Sunnyvale, CA). We revisited nests approximately every other day until failure or hatch. We captured incubating adults with a drop-door nest trap and individually marked each bird with five plastic bands. Once hatched, we individually marked each chick with three plastic bands. To prevent leg injuries (Amirault et al. 2006), we did not seal our plastic bands. While some partial band loss was recorded (1 or more bands), it was fairly infrequent (range: 5 – 13 birds yr⁻¹, 2006 – 2008), indicating that there could

be a slight negative bias in our survival estimates. We attempted to resight banded birds every two days throughout the breeding season (April – August) on the primary study sandbars (n = 16). Additionally, we visited most other sandbars on the reach approximately 2 – 3 times each year to resight banded birds. We attempted to determine the nesting status of all returning banded individuals. We considered an individual a known breeder if we captured the bird on a nest or we resighted the bird incubating or brooding chicks. We further classified nesters according to the sandbar type (engineered, natural) on which they nested. If a bird was sighted or trapped on more than one nest during the breeding season, we used the location of the first breeding attempt to determine the nesting status for that year. This study includes banding from 2005 – 2007 and resightings from 2006 - 2008.

WINTER BAND RESIGHTINGS

We used a mixture of volunteer and agency efforts to locate our birds during the non-breeding season. Piping plovers winter along the U.S. coast from North Carolina to Texas and also are found in Mexico and the Caribbean (Elliot-Smith and Haig 2004). Although most of our winter resightings were incidental, some were from regular surveys (Gratto-Trevor et al., unpublished manuscript).

ESTIMATING NEST DENSITY AND WATER DISCHARGE

Based on field observations, we hypothesized that population density and water discharge might have affected piping plover survival and movement. We estimated habitat availability using land classification coverages collected during the 2005 – 2007 breeding seasons (L. Strong, US Geological Survey, unpublished data). Pan-sharpened multispectral QuickBird imagery was collected each year (between April and October) and classified using Definens Developer Software for a concurrent study of least tern (*Sternula antillarum*) and piping plover sandbar habitat availability (L. Strong, unpublished data). The amount of suitable nesting habitat was calculated as the amount of open and sparsely vegetated wet and dry sand habitat on a sandbar, and the amount of suitable foraging habitat was calculated as the amount of open and sparsely vegetated wet substrate. From our nest monitoring data, we calculated the maximum number of nests active at one time on each sandbar and summed the habitat availability and number of active nests to estimate the average nesting density on natural and engineered sandbars. We obtained information on water releases from the Gavins Point Dam (USACE 2008) as an index to water levels.

ESTIMATING APPARENT SURVIVAL AND WITHIN-SITE MOVEMENT

All survival analyses were performed in Program Mark. We used multi-strata models to simultaneously calculate apparent survival (ϕ), resight (p) and transition rates (Ψ , rates that measure the probabilities that an individual will move among multiple strata; Hestbeck et al. 1991, Brownie et al. 1993).

We estimated survival and movement of piping plovers nesting on natural (N) and engineered (E) sandbars using a multi-strata model. Because the nesting locations of all adults were not known in each year, we also estimated survival and movement for an unknown nesting status stratum (U). We analyzed data from individuals captured as chicks and those captured as adults separately. Although chicks were considered adults after year one, we continued to analyze them separately from adults (i.e. plovers banded as chicks were modeled separately from those banded as adults regardless of their returning as an adult). The three strata were similar for chicks (N, E, U), but the capture-year stratum was defined by the sandbar type on which a bird hatched. In both cases, no individuals entered the study in the unknown stratum since all adults were initially captured on nests, and all chicks were from known nests; therefore there are no parameter estimates for the unknown stratum for adults in the first year of the study or chicks in any year.

For adults, we began modeling with year-specific (yr) variation in each parameter in each of the three strata ($g \cdot yr$, where g represents stratum [i.e., group: N, E, U], and \cdot represents a multiplicative relationship). We used the median c -hat test on the global model in Program Mark to estimate and correct for overdispersion and Akaike's Information criterion, corrected for small sample sizes and overdispersion (QAIC_c, Burnham and Anderson 2002) to rank and evaluate further models.

To develop the model set, we created models with reduced complexity. The movement of adults from the unknown stratum or vice versa was most likely a function of our ability to determine where the bird nested, and our efforts to determine nesting status were relatively invariant from year to year. Therefore, we assumed that both the transition probabilities from the known nesting strata to the unknown nesting strata (i.e., Ψ_{NU} , Ψ_{EU}) and the transition probabilities from the unknown strata to the two known strata (i.e., Ψ_{UN} , Ψ_{UE}) were constant, represented as (\cdot), with respect to year. We tested several structures for recapture (p), transition (Ψ), and apparent survival (ϕ) rates (Table 1). We began by testing structures for the recapture

rate (p) and used the model with the lowest QAIC_c value and repeated this process for transition rates (Ψ) and then apparent survival rates (ϕ).

For birds banded as chicks, we began modeling with yearly variation (yr) for parameters for the chicks in each stratum ($a1*yr*g$, where $a1$ stands for age and indicates a difference between chicks and chicks that returned as adults, g represents stratum [N, E, U], and $*$ represents a multiplicative relationship) and a constant estimate for chicks that survived and returned within each strata. We used the median c -hat test in Program Mark to estimate overdispersion ($c\text{-hat} < 1.0$, no correction) and Akaike's Information criterion, corrected for small sample sizes (AIC_c, Burnham and Anderson 2002) to rank and evaluate further models. Because first-year adults may not breed (Elliot-Smith and Haig 2004), meaning that the unknown stratum measures relative breeding propensity for chicks that survive and return, we did not assume that the probability of transition from known to unknown strata (Ψ_{NU} , Ψ_{EU}) or the converse (Ψ_{UN} , Ψ_{UE}) was constant. We tested similar structures for recapture (p), transition (Ψ), and apparent survival (ϕ) rates as with adults (Table 1). We began by testing structures for the recapture rate (p), choosing the model with the lowest AIC_c value and repeating the process for transition (Ψ) and apparent survival (ϕ) rates. We added individual covariates to the structural model with the lowest AIC_c value to test for the effect of nesting density (D_{NEST} , maximum active nests/ha of nesting habitat) and foraging density (D_{FOR} , maximum active nests/ha of foraging habitat) on survival and movement and of age at banding (A) and hatch date (H) on survival.

ESTIMATING SURVIVAL AND SITE FIDELITY

We investigated survival and fidelity to the study area with Barker's (1997) live/dead encounter model. The Barker model uses supplemental information from band recoveries or off-site band resightings to separate survival from emigration to obtain an unbiased survival estimate (Barker 1997). The Barker model estimates true survival (S , different from apparent survival ϕ), recapture probability (p), reporting rate of dead encounters (r), the resight rate of individuals during supplemental intervals (R), the mortality rate of birds sighted during the supplemental period (R'), the fidelity of individuals to the study area (F), and the return rate of individuals that have emigrated (F'). We modeled individuals banded as chicks and those banded as adults separately.

For adults we began with a model where each parameter varied by year (yr). We did not use sandbar type in this analysis because the nesting locations of all adults were not known in each year. We fixed the reporting rate of dead birds (r) to zero, because there were no reports of dead birds from off the site. We fixed the return rate of emigrants (F') to zero, such that all emigration was assumed permanent. We used the median c -hat test in Program Mark to estimate and correct for overdispersion and Akaike's Information criterion, corrected for small sample sizes and overdispersion (QAIC_c, Burnham and Anderson 2002) to rank and evaluate further models. We proceeded by testing a constant structure (.) for recapture rate (p) using the model with the lowest QAIC_c value, and repeating the process for the other parameters, R , R' , F , and S .

For the individuals banded as chicks, we began with a model where each parameter varied by group and year ($a1*g*yr$, where $a1$ (i.e. age) indicates a difference between chicks and chicks that returned as adults, g represents group, *viz.* hatched on engineered sandbar or hatched on natural sandbar, and $*$ represents a multiplicative relationship). As with the adults, we fixed the reporting rate of dead birds (r) and the return rate of emigrants (F') at zero. To improve the estimability of the other parameters, we also assumed that the value for R' did not vary by age, group, or year (.). We used the median c -hat test in Program Mark to estimate and correct for overdispersion and Akaike's Information criterion, corrected for small sample sizes and overdispersion (QAIC_c, Burnham and Anderson 2002) to rank and evaluate further models. We tested several structures for p , R , F , and S (Table 1). We began by testing structures for p , selecting the one with the lowest QAIC_c and repeating the process for R , F , and S . As with the multi-strata model, we tested the effect of nesting density (D_{NEST}) and foraging density (D_{FOR}) on survival and site fidelity and of age-at-banding (A) and hatch date (H) on survival in the model for individuals banded as chicks.

PARAMETER ESTIMATES

From the resulting multi-strata and Barker (1997) model sets, two for birds banded as adults and two for birds banded as chicks, we obtained model-averaged parameter estimates and unconditional standard errors (Burnham and Anderson, 2002). If the competing model(s) (likelihood ≥ 0.125 ; Burnham and Anderson 2002) did not contain year-, group-, or age-specific variation, we created a single Monte Carlo estimate from year-, group-, and age-specific model-averaged parameter estimates by randomly selecting from the model-averaged distributions 10 000 times and taking the mean and standard error of the results. We use the term “apparent

survival (ϕ)” for estimates from the multi-strata model, indicating that emigration is not accounted for in these estimates (Sandercock 2006). We use “survival (S)” for estimates from Barker’s (1997) unbiased estimate of survival. When interpreting the difference between individual estimates, we compared the unconditional confidence intervals and model-averaged point estimates. If either of the intervals included the other point-estimate, we interpreted this as relatively little evidence there being difference between the two estimates.

Results

CAPTURE, BANDING, AND RETURNS

From 2005 – 2007, we banded 357 adult piping plovers and 685 chicks. On average, chicks were 2.6 days old (2.4 – 2.8) at banding and hatched on 26 June (CI₉₅: 25 June – 27 June). Birds banded as adults were first sighted in years after banding on average on 25 April (CI₉₅: 23 April – 28 April, N = 106), 29 April (CI₉₅: 27 April – 01 May, N = 195), and 01 May (CI₉₅: 28 April – 03 May, N = 245) in 2006, 2007, and 2008, respectively. One-year-old adults were first sighted approximately one month later, 30 May (CI₉₅: 21 May – 07 June, N = 37), 28 May (CI₉₅: 19 May – 06 June, N = 15), and 1 June (CI₉₅: 27 May – 06 June, N = 39) in 2006, 2007, and 2008 respectively.

SUPPLEMENTAL SIGHTINGS

We received reports of 169 marked birds on the wintering grounds. Sightings ranged from South Carolina to Texas, but most (93%) were seen on the coast of the Gulf of Mexico. We also received reports of 8 plovers nesting outside of our study area as far north as Lake of the Woods, Ontario and as far south as the Lower Platte River, Nebraska. No birds were known to breed outside the Great Plains region.

ADULT SURVIVAL

The apparent survival (ϕ) of established nesters was not different than birds of unknown nesting status. Despite all of the competitive models (likelihood ≥ 0.125) including the distinction between known nesters and birds of unknown status (Table 2), the confidence interval for the unknown nesters included the estimate for known nesters (Table 3; Fig. 1). There was no evidence for differences in apparent survival between adults that nested on natural sandbars and those that nested on engineered sandbars (all of the competing models contained equivalent survival between the two groups, E=N, Table 2).

Survival (S) was consistent throughout the study (ca. 0.82, Tables 4 and 5; Fig. 1), and was not different than apparent survival rates from 2005 – 2006 on both engineered and natural sandbars. There was some evidence that from 2006 – 2007, apparent survival for known and unknown nesters was 0.076 and 0.136 less than survival, respectively (Fig. 1). Two of the three competing multi-strata models contained yearly variation (Table 2), but the confidence intervals for each of these estimates contained the other point estimate (Fig. 1).

ADULT MOVEMENT

Within the study site, known nesters were more likely to leave a natural sandbar for an engineered sandbar than the converse, regardless of year ($\Psi_{NE}=0.192$ vs. $\Psi_{EN}=0.091$, Table 3). Site fidelity in the first year of the study was 100% but decreased by ca. 0.108 between 2006 and 2007 (Table 5, Fig. 2).

JUVENILE SURVIVAL

First-year apparent survival (ϕ) and survival (S) appeared to be related to age-at-banding, hatch date, an interaction between age-at-banding and hatch date, and nesting density. Although all of these parameters were in the top-ranked (lowest AIC_c value) multi-strata model (Table 6), only the effect of hatch date was significantly different from 0 ($\Delta AIC_c > 35$ for all models without hatch date; Table 7), such that chicks that hatched later in the season had a lower apparent survival than those that hatched earlier.

The results for the estimates of survival (S) were similar to those from the multi-strata model (Table 8), but the survival increased with increasing density on natural sandbars and decreased with increasing density on engineered sandbars ($\Delta QAIC_c > 10$ for model with same density dependence between groups; Table 9, Fig. 3). Hatch date was negatively correlated with survival (Fig. 4). Survival was lower in the second year of the study than in the first year (Fig. 3).

JUVENILE MOVEMENT

Chicks that hatched on engineered sandbars with greater nesting densities were more likely to move to natural sandbars than were those that hatched on engineered sandbars with lower densities (β : 0.489, 95% CI: 0.428 – 0.551). The movement to engineered sandbars of chicks that hatched on natural habitat was constant and less than the converse in the last two years of the study (Table 7). As expected, the site fidelity of juveniles was lower than that of adults (Fig. 2). Based on transition probabilities to the unknown nesting status (e.g., $1 - \Psi_{NU} = \Psi_{NE} + \Psi_{NN}$), ca.

66 – 100% of chicks that hatched on natural sandbars bred in their first year and ca. 37 – 85% of chicks that hatched on engineered sandbars did so. Fidelity of individuals from 2005 – 2006 that hatched on natural sandbars was lower than that of individuals that hatched on engineered sandbars (Fig. 2). Similar to adults, the fidelity of chicks hatched on engineered sandbars decreased from 2006 to 2007, but there was less evidence of a decline for chicks hatched on natural sandbars (Fig. 2).

NESTING DENSITY AND WATER DISCHARGE

Nesting densities on engineered sandbars were between 1.78 and 7.05 times greater than those on natural sandbars (Fig. 5). Densities on natural sandbars remained relatively constant throughout the study, but they nearly tripled on engineered sandbars in 2006 (Fig. 5). Average monthly releases from the Gavins Point dam were consistently lower than the 41-year average for the reach (Fig. 6). Water releases in 2005 remained relatively stable during the breeding season, whereas they increased steadily in 2006 and 2007 and were positively related to nesting densities for birds on engineered habitat (Fig. 6). Although releases increased through the breeding season in 2007, they were similar to 2005 during the chick rearing period (June – August; Fig. 6). In 2006, however, releases during the chick-rearing period were higher than in both 2005 and 2007 (Fig. 6).

Discussion

JUVENILE SURVIVAL

As predicted, the survival of chicks hatched on engineered sandbars decreased with increasing nesting density. The primary cause of piping plover chick mortality in this region is predation (Kruse et al. 2001), and predation reached nearly 100% on some sandbars in some years (D. Catlin, pers. obs.). Density-dependent predation has been noted in other shorebirds but mainly on the wintering grounds (Durrell 2000, Whitfield 2003a, Whitfield 2003b). Increased competition at dense sites may lead to the use of areas that have greater predation risk (Whitfield 2003b). It is also possible that the large aggregations and visible/audible intraspecific interactions of birds on these dense sites attract predators. Piping plovers in this region certainly evolved under the pressure of avian predators, but it is unknown whether such predation reached the levels that we have seen in recent years. The Missouri River originally flowed through steppe and prairie parkland (Bailey 1976) and meandered widely in its floodplain. Under these conditions it seems likely that gallery forests were less extensive and, consequently that avian

predators, such as great horned owls and crows, were more sparsely distributed and less likely to forage on river sandbars. It seems unlikely that prehistoric nesting densities were as high as those seen on the densest engineered sandbars in this study given the ephemeral nature of natural habitat, and a hydrograph that likely created sandbars more frequently and throughout more of the river than currently. Thus, pressure from avian predators may have been less in the past than at present. At current plover densities and distributions, however, a relatively small number of predators can kill a large number of piping plovers.

We found dead chicks with injuries that may have been caused by attacks from adult plovers (Catlin and Fraser, unpublished data). Although territorial defense is common in birds (Brown 1969), these altercations rarely escalate to the point that either of the competitors is killed (Maynard Smith and Price 1973). There is little risk involved for an adult attacking an unrelated chick, except when the parents of that chick are present to defend it. However, if at increased densities parental attention is otherwise occupied, unrelated adults could attack chicks without serious confrontation. The killing of unrelated young can occur when food is limited (Ashbrook et al. 2008), presumably to reduce competition. Piping plover growth rates were relatively low in 2006 and in general were negatively related to nesting densities (Catlin and Fraser unpublished data), suggesting that agonism could have contributed to the density-dependent mortality on engineered sandbars.

Contrary to our findings on engineered sandbars, chicks on natural sandbars had higher survival at higher densities. Plover numbers and densities were generally lower on natural sandbars than on engineered sandbars, and the difference in the effect of density on the two habitat types could reflect a threshold effect or non-linearity in the effects of density on chick survival (Murray 1994), or it could indicate that habitat differences produced a fundamentally different relationship between density and survival. The numbers or density of young on natural sandbars may have been too low to invite severe predation or agonism. Great-horned owls are opportunistic, but they can specialize on prey in situations of high food abundance (Houston et al. 1998). Great-horned owls generally hunt in open areas (Houston et al. 1998). Moreover, recently fledged young owls may chase prey on foot in open areas such as fields (Dunstan 1970), and presumably sandbars. For these reasons, the more densely vegetated natural sandbars, with smaller open areas, may be less hospitable to foraging owls than the relatively open engineered sandbars.

ADULT SURVIVAL

Overall, adult survival rates were higher than most estimates for other populations (Wilcox 1959, Loegering 1992, USFWS 1996, Larson et al. 2000, Cohen et al. 2006), but only two other studies estimated true survival (Cohen et al. 2006, LeDee 2008). Cohen et al. (2006) calculated survival for a small population of piping plovers nesting on the Atlantic coast. Cohen et al.'s (2006) point estimate was 7 – 18 % lower than this study's value (Table 10). LeDee's (2008) estimate was from a relatively small population of piping plovers nesting on the shores of the Great Lakes. LeDee (2008) estimated a true survival of 0.91 (Table 10), which is 9% higher than our estimate. Small sample sizes in both of these studies contributed to wide confidence intervals, but the differences among point estimates were substantial. If survival is negatively related to overall population density (Newton 1998; Paradis et al. 2002, Tavecchia et al. 2007), then these differences in survival may be explained by the stages of population growth of each of the populations. In Cohen et al. (2006), the population on the barrier island had reached a plateau and was declining as a result of habitat loss during the study. The Great Lakes population, though small, was increasing during LeDee's (2008) study (Haig et al. 2005). Since 1996, the number of piping plovers on the Missouri River in South Dakota has been increasing (Haig et al. 2005), but yearly adult censuses performed by the USACE indicated that the population was stationary or nearly so during our study (G. Pavelka, USACE, personal communication). We did not directly test for an effect of density on adult survival, but the similarity of adult apparent survival between less dense, natural sandbars and more dense engineered sandbars suggests that, within our study, density was not affecting adult survival.

HABITAT QUALITY AND MOVEMENT

The lower nesting densities on natural sandbars relative to engineered sandbars suggest that piping plovers may perceive the natural sandbars to be of lower quality. First-year piping plovers, however, appeared to move to these sites at a greater rate than to the engineered sites. Young breeding birds often recruit to marginal habitat, possibly because they lack the experience to compete with older birds for the better habitat (Greenwood and Harvey 1982). In this study, first-year piping plovers arrived approximately 1 month later than adult birds, possibly after most of the best territories had been occupied by older birds. The greater movement of adult birds from natural to engineered than from engineered to natural habitat also could have precluded juveniles from finding territories on engineered sandbars. In support of this conclusion, chicks

from high density engineered sandbars were more likely to recruit to natural sandbars than those from low density engineered sandbars. Thus, the natural sandbars may represent marginal, but readily available, and easily obtained breeding habitat for younger birds recruiting to the population.

Although we did not directly test the effects of density on adult movements because of incomplete nesting records for banded birds, the consistent rate of movement from natural to engineered habitat suggests that the high densities on engineered sandbars did not prevent movements of adults to engineered habitat. With approximately 18% annual adult mortality, however, space could be consistently available to the earlier-arriving adults. Piping plovers evolved in the relatively ephemeral habitats of barrier islands, prairie lakes, and river sandbars. In such systems, habitat quality is highly variable in time and space. Therefore, plovers are adapted to a system where pioneering new areas when openings occur is likely to be adaptive.

HABITAT QUALITY AND SITE FIDELITY

Despite the relationship between within-study area movements and density, we did not find a relationship between density and the site fidelity of juveniles to the study area. As expected, juvenile piping plovers had lower site fidelity than adults. Natal dispersal is commonly greater than breeding dispersal (Greenwood and Harvey 1982, Johnson and Gaines 1990). Inbreeding avoidance often is cited as the reason for the difference in fidelity rates between adults and juveniles, particularly when natal dispersal is sex-biased (Greenwood and Harvey 1982, Johnson and Gaines 1990), but reducing kin competition is an alternative hypothesis (Bowler and Benton 2005).

The lower fidelity to the study area of birds that hatched on natural sandbars than those that hatched on engineered sandbars, however, suggests that something in addition to inbreeding avoidance or kin competition is affecting juvenile fidelity. The major difference between natural and engineered sandbars may only be the age of the habitat. The engineered habitat was 1- 3 years old during the study, whereas, most of the natural habitat was 8 – 10 years old. Several lines of evidence suggested that natural sandbars were less desirable to piping plovers than engineered sandbars. Adults were more likely to move from a natural to an engineered sandbar than the converse, nesting densities on natural sandbars were much lower than those on engineered sandbars, and adults selected for engineered habitat preferentially when choosing nest sites (Chapter 1). For this preference to be adaptive, birds nesting on engineered habitat ought to

have higher fitness than birds nesting on natural sandbars. Engineered sandbars did have a higher nesting success than natural sandbars during this study (Chapter 1), which could lead to higher reproductive output for those birds nesting on engineered sandbars in conjunction with equivalent chick survival. With increasing density, however, these engineered sandbars could become ecological traps (Gates and Gysel 1978) because of decreased juvenile survival at high nesting densities. Therefore, if the major difference between engineered and natural habitat is age, then there needs to be a consistent creation of new high-quality habitat to support piping plovers. Again, given the ephemeral prehistoric nature of their habitat, it stands to reason that piping plovers have evolved to capitalize on these new habitats.

We also found a general pattern of reduced site fidelity in 2006, regardless of plover age and habitat type. Low reproductive success often leads to decreased fidelity in adult birds (Greenwood and Harvey 1982, Johnson and Gaines 1990, Wiklund 1996, Gowaty and Plissner 1997, Haas 1998, Catlin et al. 2005). In this study, reproductive success was significantly lower in 2006 than in 2005 as a result of predation, which may have contributed to the decreased site fidelity, at least for adult plovers. Since the decline in site-fidelity was evident in both adults and juveniles, however, there would have to be some way for the post-fledging juveniles to evaluate the overall reproductive success of a site prior to migration. Fledgling piping plovers were seen in relatively large flocks at times (D. Catlin, pers. obs.), and these groups could potentially acquire that information through size and density. The use of conspecific reproductive success to evaluate future reproductive success has been seen in other birds (Danchin et al. 1998, Brown et al. 2000, Doligez et al. 2002, H  naux et al. 2007, Boulinier et al. 2008). In a long-term study of great cormorant (*Phalacrocorax carbo sinensis*) survival and movement, the probability of young individuals leaving their natal area was more related to the reproductive success at its natal colony than the reproductive success at the colony to which it dispersed (H  naux et al. 2007). H  naux et al. (2007) found a similar but weaker effect in experienced breeders, owing potentially to the benefits of colony experience. Similarly, we found that the reduction in site fidelity for experienced breeders was less pronounced than that for first-year birds. If the decrease in site fidelity that we saw between 2005 and 2006 was related to poor reproductive success, breeding experience could have reduced the effect on adult piping plovers since all adult plovers had at least one year's breeding experience.

Water discharge and density also may have affected overall site fidelity in 2006. Despite the lack of evidence supporting an effect of density on juvenile site fidelity, nesting density on engineered sandbars was nearly three times higher in 2006 than in 2005. Between 2005 and 2006, the amount of nesting habitat on engineered sandbars decreased substantially. While some of this decrease in habitat was as a result of erosion and vegetation encroachment, some was also due to higher water in 2006 than in 2005. The flow of water on the Gavins Point Reach is largely a function of the output from the dam and the James River, particularly in late spring or early summer (April – June). Flows throughout the study period were below the 41-year average, but within the study period were highest during the 2006 chick-rearing period (June – August). In extreme years, river flow can reduce piping plover reproductive output by flooding nests and broods (Higgins and Brashier 1993, Kruse and Pavelka 1996, Plissner and Haig 2000). Flooding also would lead to a reduction in territory size and perhaps a total loss of some territories. Therefore, regional declines in population numbers that were attributed to reproductive failure (Plissner and Haig 2000) may have been exacerbated by reduced breeding habitat and increased density leading to decreases in adult and juvenile fidelity. Moreover, the increase in water discharge and in density was related to a decrease in growth rates of piping plover chicks (Catlin and Fraser unpublished data), which could have either directly affected fidelity of adults and juveniles, or done so indirectly through reproductive success.

CONCLUSIONS

Our results suggested that engineered habitat was suitable habitat for nesting piping plovers. Adult piping plovers moved from natural sandbars to engineered sandbars with a greater probability than the converse, suggesting that engineered habitat appeared to be of greater quality than natural habitat. Movement rates into engineered habitat remained high, even when reproductive success had decreased and density had increased substantially, suggesting that there was a disconnect between habitat selection and fitness. If owl predation has recently become an issue or has recently become more pronounced, then perhaps piping plovers are not yet equipped to evaluate habitat appropriately. Movement and reproductive output were related to nesting density, such that movement was greater and reproductive success was lower on more densely-populated engineered sandbars than on less-densely populated engineered sandbars. Our results indicate that engineered habitat could be used to mitigate habitat limitation in piping plovers and potentially in other shorebirds as well.

Conservation efforts often ignore the effects of population density on population dynamics because of the difficulty in determining such effects. Understanding the factors limiting population growth, however, is an extremely important aspect to the development of realistic habitat and population recovery goals. For instance, meeting population recovery goals would require more natural habitat than engineered habitat based on the observed densities of the two habitat types. The effects of increased density on engineered habitat, however, may produce negative consequences for recovery by reducing juvenile survival and potentially increasing emigration. If density-dependent interactions are ignored, the USACE's habitat creation program could serve as an ecological trap (Gates and Gysel 1978), absorbing large numbers of birds but reducing reproductive success through increased density. In order for this to occur, however, plovers would have to remain on these sites despite low reproductive success. We need to examine the individual dispersal responses to reproductive failure to determine if this is the case. Our results highlight the importance of evaluating population density in conservation planning and of considering the potential pitfalls of using habitat selection to determine the success of conservation measures.

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Table 1: Definitions of basic model structures for the Multi-strata model parameters (ϕ , p , Ψ) and the Barker (1997) model parameters (S , p , R , R' , F , F') of piping plover survival and movement for adults and chicks on the Gavins Point Reach and Lewis and Clark Lake on the Missouri River. Strata represent the groups in the multi-strata model for both adults and chicks (known nesting on natural [N] or engineered [E] sandbars and unknown nesting status [U]), and group represents the sandbar type from which a chick hatched (natural or engineered).

Age ^A	Parameter	
	Structure	Definition
Adult	$g*yr$	Stratum-specific estimates, multiplicative effect of year, global model
	$g+yr$	Stratum specific estimates, additive effect of year
	$E=N*yr$	Estimate for known nesting strata is equal and different from unknown nesting stratum, multiplicative effect of year
	$E=N+yr$	Estimate for known nesting strata is equal and different from unknown nesting stratum, additive effect of year
	g	Stratum specific estimates
	yr	Year-specific estimates
	.	Constant
Chick	$a1*g*yr$	Age- and group/stratum-specific estimates, multiplicative effect of year, global model
	$a1*g+yr$	Age- and group/stratum-specific estimates, additive effect of year
	$a1*g$	Age- and group/stratum-specific estimates
	$a1$	Age-specific estimates
	ca	Estimates for chicks that survived to adulthood are equal among groups

Table 2: Model rankings for an analysis of multi-strata capture-mark-recapture models for survival (ϕ), resight (p) and movement (Ψ) of piping plovers banded as adults (N = 357) on the Gavins Point Reach of the Missouri River and Lewis and Clark Lake from 2005 – 2008.

Model ^A	ΔQAIC_c^B	Weight	Likelihood	K	Deviance
$\phi (E=N*yr)p(g)\Psi_{NE}(\cdot)\Psi_{EN}(\cdot)\Psi_{NU}=\Psi_{EU}(\cdot)\Psi_{UN}=\Psi_{UE}(\cdot)$	0.000	0.549	1.000	12	129.068
$\phi(E=N+yr)p(g) \Psi_{NE}(\cdot)\Psi_{EN}(\cdot)\Psi_{NU}=\Psi_{EU}(\cdot)\Psi_{UN}=\Psi_{UE}(\cdot)$	1.365	0.277	0.505	10	134.583
$\phi(E=N)p(g) \Psi_{NE}(\cdot)\Psi_{EN}(\cdot)\Psi_{NU}=\Psi_{EU}(\cdot)\Psi_{UN}=\Psi_{UE}(\cdot)$	3.129	0.115	0.209	9	138.412
$\phi(g*yr)p(g) \Psi_{NE}(\cdot)\Psi_{EN}(\cdot)\Psi_{NU}=\Psi_{EU}(\cdot)\Psi_{UN}=\Psi_{UE}(\cdot)$	5.285	0.039	0.071	15	128.077
$\phi (g*yr)p(g) \Psi_{NE}(\cdot)\Psi_{EN}(yr)\Psi_{NU}=\Psi_{EU}(\cdot)\Psi_{UN}=\Psi_{UE}(\cdot)$	7.494	0.013	0.024	17	126.067
$\phi (g*yr)p(g) \Psi_{NE}(yr)\Psi_{EN}(yr)\Psi_{NU}=\Psi_{EU}(\cdot)\Psi_{UN}=\Psi_{UE}(\cdot)$	10.631	0.003	0.005	19	124.958
$\phi (g*yr)p(g*yr) \Psi_{NE}(yr)\Psi_{EN}(yr)\Psi_{NU}=\Psi_{EU}(\cdot)\Psi_{UN}=\Psi_{UE}(\cdot)$	11.769	0.002	0.003	21	121.822
$\phi (g*yr)p(\cdot)\Psi_{NE}(yr)\Psi_{EN}(yr)\Psi_{NU}=\Psi_{EU}(\cdot)\Psi_{UN}=\Psi_{UE}(\cdot)$	12.432	0.001	0.002	17	131.005
$\phi (g*yr)p(g+yr) \Psi_{NE}(yr)\Psi_{EN}(yr)\Psi_{NU}=\Psi_{EU}(\cdot)\Psi_{UN}=\Psi_{UE}(\cdot)$	12.441	0.001	0.002	20	124.636
$\phi (g*yr)p(yr) \Psi_{NE}(yr)\Psi_{EN}(yr)\Psi_{NU}=\Psi_{EU}(\cdot)\Psi_{UN}=\Psi_{UE}(\cdot)$	16.456	0.000	0.000	19	130.784
$\phi (g*yr)p(g*yr) \Psi_{NE}(yr)\Psi_{EN}(yr)\Psi_{NU}(yr)\Psi_{EU}(yr)\Psi_{UN}(yr)\Psi_{UE}(yr)$	23.479	0.000	0.000	29	116.153

^A Model structure for apparent survival (ϕ), resight rate (p), and transition rates (Ψ_{NE} from natural to engineered sandbars, Ψ_{NU} from natural sandbars to unknown status, etc.). The groups (g) represent three strata: birds nesting on engineered sandbars (E), birds nesting on natural sandbars (N), and birds of unknown nesting status (U). (yr) – year-specific variation, (.) – constant.

^B Minimum $\text{QAIC}_c = 1323.726$, c-hat = 1.248

Table 3: Monte-Carlo estimates of apparent survival (ϕ), resight rate (p), and transition rates (Ψ) for piping plovers banded as adults ($N = 357$) from multi-strata model-averaged parameter estimates and unconditional standard errors on the Gavins Point Reach of the Missouri River and Lewis and Clark Lake from 2005 – 2008.

Parameter	Period	Estimate ^A	Standard Error	Lower 95% Confidence Limit	Upper 95% Confidence Limit
$\phi_{\text{engineered, natural}}$	2005 - 2006	0.824	0.039	0.748	0.899
	2006 - 2007	0.748	0.041	0.667	0.830
ϕ_{unknown}	2005 - 2006	NA	NA	NA	NA
	2006 - 2007	0.688	0.116	0.434	0.864
$p_{\text{engineered}}$	2005 - 2007	0.999	0.006	0.989	1.000
p_{natural}	2005 - 2007	0.891	0.043	0.807	0.975
p_{unknown}	2006 - 2007	0.999	0.002	0.996	1.000
$\Psi_{\text{NE}}^{\text{B}}$	2005 - 2008	0.192	0.033	0.128	0.257
$\Psi_{\text{NU, EU}}^{\text{B}}$	2005 - 2008	0.234	0.050	0.135	0.332
$\Psi_{\text{EN}}^{\text{B}}$	2005 - 2008	0.091	0.021	0.050	0.131
$\Psi_{\text{UN, UE}}^{\text{B}}$	2005 - 2008	0.342	0.039	0.264	0.419

^A Estimates and standard errors for estimates that are not both year- and group-specific were derived from Monte-Carlo procedure with 10,000 iterations to combine year- and group-specific estimates.

^B Transition from nesting on a natural sandbar to an engineered sandbar (NE), nesting on an engineered sandbar to a natural sandbar (EN), nesting on a natural sandbar to unknown nesting status (NU), nesting on an engineered sandbar to unknown nesting status (EU), unknown nesting status to a natural sandbar (UN), and unknown nesting status to an engineered sandbar (UE).

Table 4: Model rankings for an analysis of Barker (1997) capture-mark-recapture models for survival (S) and site fidelity (F) of piping plovers banded as adults (N = 357) on the Gavins Point Reach of the Missouri River and Lewis and Clark Lake from 2005 – 2008.

Model ^A	ΔQAIC_c^B	Weight	Likelihood	K	Deviance
S(.)p(.)R(.)R'(.)F(yr)	0.000	0.770	1.000	7	84.863
S(yr)p(.)R(.)R'(.)F(yr)	3.940	0.107	0.140	9	84.741
S(yr)p(.)R(yr)R'(.)F(yr)	4.622	0.076	0.099	11	81.346
S(yr)p(.)R(.)R'(.)F(.)	6.734	0.027	0.035	8	89.567
S(yr)p(.)R(yr)R'(yr)F(yr)	8.339	0.012	0.016	13	80.970
S(yr)p(yr)R(yr)R'(yr)F(yr)	9.609	0.006	0.008	14	80.188
S(yr)p(.)R(.)R'(yr)F(yr)	13.163	0.001	0.001	11	89.887

^A Model structure for true survival (S), resight rate on the breeding grounds (p), resight rate during the nonbreeding season (R), the mortality rate of birds that were sighted during the non-breeding season (R'), and the fidelity rate (F). (yr) – year-specific variation.

^B Minimum $\text{QAIC}_c = 817.244$, $\hat{c} = 2.044$

Table 5: Monte Carlo estimates from model-averaged parameter estimates and unconditional standard errors from the Barker (1997) model for piping plovers banded as adults (N = 357) on the Gavins Point Reach of the Missouri River and Lewis and Clark Lake from 2005 – 2008.

Parameter ^A	Period	Estimate ^B	Standard Error	Lower 95% Confidence Limit	Upper 95% Confidence Limit
S	2005 - 2006	0.822	0.033	0.747	0.878
	2006 - 2007	0.824	0.038	0.736	0.887
p	2005 - 2007	0.971	0.015	0.941	1.000
R	2005 - 2007	0.213	0.032	0.151	0.275
R'	2005 - 2007	0.118	0.028	0.063	0.174
F	2005 - 2006	0.999	0.010	0.980	1.000
	2006 - 2007	0.891	0.052	0.742	0.959

^A True survival (S), resight rate on the breeding grounds (p), resight rate during the non-breeding season (R), the mortality rate of birds that were sighted during the non-breeding season (R'), and the fidelity rate (F).

^B Estimates and standard errors for estimates that are not both year- and group-specific were derived from Monte-Carlo procedure with 10,000 iterations to combine year- and group-specific estimates.

Table 6: Model rankings for multi-strata capture-mark-recapture models for first year and adult apparent survival (ϕ), resight (p), and movement (Ψ) of piping plovers banded as chicks ($N = 685$) on the Gavins Point Reach of the Missouri River and Lewis and Clark Lake from 2005 – 2008.

Model ^A	ΔAIC_c^B	Weight	Likelihood	K
$\phi(a1*g+yr+A*H+g*D_{NEST})p(a1*g,ca)\Psi_{NE}(a1)\Psi_{NU}(a1*yr)\Psi_{EN}(a1*yr+D_{NEST})\Psi_{EU}(a1*yr)\Psi_{UN}(a1)=\Psi_{UE}(a1)$	0.000	0.422	1.000	31
$\phi(a1*g+yr+A*H+D_{NEST})p(a1*g,ca)\Psi_{NE}(a1)\Psi_{NU}(a1*yr)\Psi_{EN}(a1*yr+D_{NEST})\Psi_{EU}(a1*yr)\Psi_{UN}(a1)=\Psi_{UE}(a1)$	1.313	0.219	0.519	30
$\phi(a1*g+yr+A*H)p(a1*g,ca)\Psi_{NE}(a1)\Psi_{NU}(a1*yr)\Psi_{EN}(a1*yr+D_{NEST})\Psi_{EU}(a1*yr)\Psi_{UN}(a1)=\Psi_{UE}(a1)$	1.905	0.163	0.386	29
$\phi(a1*g+yr+A+H)p(a1*g,ca)\Psi_{NE}(a1)\Psi_{NU}(a1*yr)\Psi_{EN}(a1*yr+D_{NEST})\Psi_{EU}(a1*yr)\Psi_{UN}(a1)=\Psi_{UE}(a1)$	2.205	0.140	0.332	28
$\phi(a1*g+yr+A*H+D_{FOR})p(a1*g,ca)\Psi_{NE}(a1)\Psi_{NU}(a1*yr)\Psi_{EN}(a1*yr+D_{NEST})\Psi_{EU}(a1*yr)\Psi_{UN}(a1)=\Psi_{UE}(a1)$	4.074	0.055	0.130	30
$\phi(a1*g+yr+A)p(a1*g,ca)\Psi_{NE}(a1)\Psi_{NU}(a1*yr)\Psi_{EN}(a1*yr+D_{NEST})\Psi_{EU}(a1*yr)\Psi_{UN}(a1)=\Psi_{UE}(a1)$	35.151	0.000	0.000	27
$\phi(a1*g+yr)p(a1*g,ca)\Psi_{NE}(a1)\Psi_{NU}(a1*yr)\Psi_{EN}(a1*yr+D_{NEST})\Psi_{EU}(a1*yr)\Psi_{UN}(a1)=\Psi_{UE}(a1)$	36.733	0.000	0.000	26
$\phi(a1*g+yr)p(a1*g,ca)\Psi_{NE}(a1)\Psi_{NU}(a1*yr)\Psi_{EN}(a1*yr+D_{NEST})\Psi_{EU}(a1*yr+D_{FOR})\Psi_{UN}(a1)=\Psi_{UE}(a1)$	37.290	0.000	0.000	27
$\phi(a1*g+yr)p(a1*g,ca)\Psi_{NE}(a1)\Psi_{NU}(a1*yr)\Psi_{EN}(a1*yr+D_{NEST})\Psi_{EU}(a1*yr+D_{NEST})\Psi_{UN}(a1)=\Psi_{UE}(a1)$	38.760	0.000	0.000	27

$\phi(a1*g+yr)p(a1*g,ca)\Psi_{NE}(a1)\Psi_{NU}(a1*yr)\Psi_{EN}(a1*yr)\Psi_{EU}(a1*yr)\Psi_{UN}(a1)=\Psi_{UE}(a1)$	43.685	0.000	0.000	25
$\phi(a1*g+yr)p(a1*g,ca)\Psi_{NE}(a1)\Psi_{NU}(a1*yr)\Psi_{EN}(a1*yr+D_{FOR})\Psi_{EU}(a1*yr)\Psi_{UN}(a1)=\Psi_{UE}(a1)$	44.120	0.000	0.000	26
$\phi(a1*yr)p(a1*g,ca)\Psi_{NE}(a1)\Psi_{NU}(a1*yr)\Psi_{EN}(a1*yr)\Psi_{EU}(a1*yr)\Psi_{UN}(a1)=\Psi_{UE}(a1)$	45.187	0.000	0.000	24
$\phi(a1*g+yr)p(a1*g,ca)\Psi_{NE}(a1)\Psi_{NU}(a1*yr+D_{NEST})\Psi_{EN}(a1*yr)\Psi_{EU}(a1*yr)\Psi_{UN}(a1)=\Psi_{UE}(a1)$	45.531	0.000	0.000	26
$\phi(a1*g+yr)p(a1*g,ca)\Psi_{NE}(a1)\Psi_{NU}(a1*yr+D_{FOR})\Psi_{EN}(a1*yr)\Psi_{EU}(a1*yr)\Psi_{UN}(a1)=\Psi_{UE}(a1)$	45.623	0.000	0.000	26
$\phi(a1*g+yr)p(a1*g,ca)\Psi_{NE}(a1+D_{FOR})\Psi_{NU}(a1*yr)\Psi_{EN}(a1*yr)\Psi_{EU}(a1*yr)\Psi_{UN}(a1)=\Psi_{UE}(a1)$	45.765	0.000	0.000	26
$\phi(a1*g+yr)p(a1*g,ca)\Psi_{NE}(a1+D_{NEST})\Psi_{NU}(a1*yr)\Psi_{EN}(a1*yr)\Psi_{EU}(a1*yr)\Psi_{UN}(a1)=\Psi_{UE}(a1)$	45.818	0.000	0.000	26
$\phi(a1*g*yr)p(a1*g,ca)\Psi_{NE}(a1)\Psi_{NU}(a1*yr)\Psi_{EN}(a1*yr)\Psi_{EU}(a1*yr)\Psi_{UN}(a1)=\Psi_{UE}(a1)$	45.836	0.000	0.000	27
$\phi(a1*g*yr)p(a1*g,ca)\Psi_{NE}(a1)\Psi_{NU}(a1*yr)\Psi_{EN}(a1*yr)\Psi_{EU}(a1*yr)\Psi_{UN}(a1)\Psi_{UE}(a1)$	47.707	0.000	0.000	28
$\phi(a1*g*yr)p(a1*g,ca)\Psi_{NE}(a1)\Psi_{NU}(a1)\Psi_{EN}(a1*yr)\Psi_{EU}(a1*yr)\Psi_{UN}(a1)\Psi_{UE}(a1)$	48.603	0.000	0.000	26
$\phi(a1*g*yr)p(a1*g,ca)\Psi_{NE}(a1*yr)\Psi_{NU}(a1*yr)\Psi_{EN}(a1*yr)\Psi_{EU}(a1*yr)\Psi_{UN}(a1)\Psi_{UE}(a1)$	51.152	0.000	0.000	30
$\phi(a1*g*yr,ca)p(a1*g,ca)\Psi_{NE}(a1)\Psi_{NU}(a1*yr)\Psi_{EN}(a1*yr)\Psi_{EU}(a1*yr)\Psi_{UN}(a1)=\Psi_{UE}(a1)$	52.063	0.000	0.000	25
$\phi(a1*g*yr)p(a1*g*yr,ca)\Psi_{NE}(a1*yr)\Psi_{NU}(a1*yr)\Psi_{EN}(a1*yr)\Psi_{EU}(a1*yr)\Psi_{UN}(a1)\Psi_{UE}(a1)$	53.984	0.000	0.000	32
$\phi(a1*g*yr)p(a1*g,ca)\Psi_{NE}(a1)\Psi_{NU}(a1*yr)\Psi_{EN}(a1*yr)\Psi_{EU}(a1)\Psi_{UN}(a1)\Psi_{UE}(a1)$	53.997	0.000	0.000	26

$\phi(a1*g*yr)p(a1*g,ca)\Psi_{NE}(a1)\Psi_{NU}(a1*yr)\Psi_{EN}(a1)\Psi_{EU}(a1*yr)\Psi_{UN}(a1)\Psi_{UE}(a1)$	56.818	0.000	0.000	26
$\phi(a1*g*yr)p(a1*g*yr)\Psi_{NE}(a1*yr)\Psi_{NU}(a1*yr)\Psi_{EN}(a1*yr)\Psi_{EU}(a1*yr)\Psi_{UN}(a1)\Psi_{UE}(a1)$	58.200	0.000	0.000	34
$\phi(a1*g*yr)p(a1,ca)\Psi_{NE}(a1*yr)\Psi_{NU}(a1*yr)\Psi_{EN}(a1*yr)\Psi_{EU}(a1*yr)\Psi_{UN}(a1)\Psi_{UE}(a1)$	60.000	0.000	0.000	29

^A Model structure for apparent survival (ϕ), resight rate (p), and transition rates (Ψ_{NE} from natural to engineered sandbars, Ψ_{NU} from natural sandbars to unknown status, etc.). The groups (g) represent three strata: birds nesting on engineered sandbars (E), birds nesting on natural sandbars (N), and birds of unknown nesting status (U). Other values: (yr) – year-specific variation, ($a1$) first year different than adult, (A) age at banding, (H) hatch date (standardized to June 1st), (D_{NEST}) nesting density, (D_{FOR}) foraging density, and (ca) common adult value among groups.

^B Minimum $AIC_c = 989.058$; $c\text{-hat} < 1.0$, no correction.

Table 7: Monte-Carlo estimates from multi-strata model-averaged parameter estimates and unconditional standard errors for first-year and adult apparent survival (ϕ), resight rate (p), transition rates (Ψ), and the effects of individual covariates (β) for piping plovers banded as chicks ($N = 685$) on the Gavins Point Reach and Lewis and Clark Lake from 2005 – 2008.

Parameter	Period	Estimate ^A	Standard Error	Lower 95% Confidence Limit	Upper 95% Confidence Limit
ϕ adult, engineered	2006 - 2007	0.891	0.106	0.488	0.986
ϕ adult, natural	2006 - 2008	0.674	0.201	0.256	0.925
ϕ adult, unknown	2006 - 2007	0.458	0.083	0.305	0.620
p chick, engineered	2005 - 2007	1.000	0.001	0.998	1.000
p chick, natural	2005 - 2007	0.139	0.047	0.070	0.257
p adult, all	2006 - 2007	0.861	0.086	0.603	0.962
Ψ chick, NE ^B	2005 - 2008	0.141	0.060	0.059	0.302
Ψ adult, NE ^B	2006 – 2008	0.057	0.056	0.008	0.315
Ψ chick, NU ^B	2005 – 2006	0.341	0.128	0.145	0.612
	2006 – 2007	0.000	0.000	0.000	0.000
	2007 - 2008	0.142	0.085	0.040	0.394
Ψ adult, NU ^B	2006 - 2008	0.593	0.115	0.363	0.788
Ψ chick, EU ^B	2005 - 2006	0.633	0.095	0.437	0.793
	2006 - 2007	0.374	0.119	0.181	0.618
	2007 - 2008	0.151	0.019	0.118	0.191

$\Psi_{\text{adult, EU}}^B$	2006 - 2008	0.207	0.092	0.080	0.439
$\Psi_{\text{chick, EN}}^B$	2005 - 2006	0.208	0.110	0.066	0.492
	2006 - 2007	0.307	0.116	0.132	0.563
	2007 - 2008	0.756	0.019	0.716	0.792
$\Psi_{\text{adult, EN}}^B$	2006 - 2008	0.101	0.068	0.025	0.328
$\Psi_{\text{adult, UN and UE}}^B$	2005 - 2008	0.303	0.056	0.205	0.423
$\beta_{\text{hatch date}}$	2005 - 2008	-0.077	0.017	-0.110	-0.044
$\beta_{\text{age at banding}}$	2005 - 2008	-0.023	0.085	-0.189	0.143
$\beta_{\text{age at banding*hatch date}}$	2005 - 2008	0.004	0.004	-0.002	0.011
$\beta_{\text{natural nesting density}}$	2005 - 2008	0.064	0.311	-0.545	0.674
$\beta_{\text{engineered nesting density}}$	2005 - 2008	-0.279	0.265	-0.798	0.240

^A Estimates and standard errors for estimates that are not both year- and group-specific were derived from Monte-Carlo procedure with 10,000 iterations to combine year- and group-specific estimates.

^B Transition from nesting/hatched on a natural sandbar to an engineered sandbar (NE), nesting/hatched on an engineered sandbar to a natural sandbar (EN), nesting/hatched on a natural sandbar to unknown nesting status (NU), nesting/hatched on an engineered sandbar to unknown nesting status (EU), unknown nesting status to a natural sandbar (UN), and unknown nesting status to an engineered sandbar (UE).

Table 8: Model rankings for an analysis of Barker (1997) capture-mark-recapture models for first-year and adult survival (S) and site fidelity (F) of piping plovers banded as chicks (N = 685) on the Gavins Point Reach of the Missouri River and Lewis and Clark Lake from 2005 – 2008.

Model ^A	ΔQAIC_c^B	Weight	Likelihood	K
S(a1*g*yr+A*H+g*D _{NEST})p(a1*g,ca)R(a1)R'(.)F(a1*g*yr)	0.000	0.993	1.000	26
S(a1*g*yr+A*H+D _{NEST})p(a1*g,ca)R(a1)R'(.)F(a1*g*yr)	10.029	0.007	0.007	25
S(a1*g*yr+A*H)p(a1*g,ca)R(a1)R'(.)F(a1*g*yr)	16.614	0.000	0.000	24
S(a1*g*yr+A+H)p(a1*g,ca)R(a1)R'(.)F(a1*g*yr)	18.193	0.000	0.000	23
S(a1*g*yr+A*H+D _{FOR})p(a1*g,ca)R(a1)R'(.)F(a1*g*yr)	18.522	0.000	0.000	25
S(a1*g*yr+A)p(a1*g,ca)R(a1)R'(.)F(a1*g*yr)	59.314	0.000	0.000	22
S(a1*g*yr)p(a1*g,ca)R(a1)R'(.)F(a1*g*yr)	66.640	0.000	0.000	21
S(a1*g*yr)p(a1*g,ca)R(a1*g)R'(.)F(a1*g*yr)	66.829	0.000	0.000	22
S(a1*g*yr)p(a1*g,ca)R(a1)R'(.)F(a1*yr)	68.087	0.000	0.000	19
S(a1*g*yr)p(a1*g,ca)R(a1)R'(.)F(a1*g*yr,ca)	68.476	0.000	0.000	20
S(a1*g*yr)p(a1*g,ca)R(a1)R'(.)F(a1*g*yr+g*D _{NEST})	68.850	0.000	0.000	23
S(a1*g*yr,ca)p(a1*g,ca)R(a1)R'(.)F(a1*g*yr)	69.177	0.000	0.000	20
S(a1*g*yr)p(a1*g,ca)R(a1)R'(.)F(a1*g+yr)	69.277	0.000	0.000	20
S(a1*g*yr)p(a1*g,ca)R(a1)R'(.)F(a1*g*yr+D _{NEST})	71.446	0.000	0.000	22
S(a1*g*yr)p(a1*g,ca)R(a1)R'(.)F(a1*g*yr+D _{FOR})	72.269	0.000	0.000	22
S(a1*g*yr)p(a1*g,ca)R(a1*g*yr)R'(.)F(a1*g*yr)	72.317	0.000	0.000	26
S(a1*g*yr)p(a1*g,ca)R(a1*g*yr,ca)R'(.)F(a1*g*yr)	73.426	0.000	0.000	25
S(a1*g*yr)p(a1)R(a1*g*yr)R'(.)F(a1*g*yr)	73.555	0.000	0.000	25

S(a1*g*yr)p(a1*g*yr,ca)R(a1*g*yr)R'(.)F(a1*g*yr)	73.734	0.000	0.000	28
S(a1*g*yr)p(a1*g*yr)R(a1*g*yr)R'(.)F(a1*g*yr)	75.136	0.000	0.000	29
S(a1*g*yr)p(a1*g,ca)R(a1)R'(.)F(a1*g)	76.011	0.000	0.000	20
S(a1*yr)p(a1*g,ca)R(a1)R'(.)F(a1*g*yr)	91.526	0.000	0.000	20
S(a1*g+yr)p(a1*g,ca)R(a1)R'(.)F(a1*g*yr)	92.881	0.000	0.000	21

^A Model structure for true survival (S), resight rate on the breeding grounds (p), resight rate during the nonbreeding season (R), the mortality rate of birds that were sighted during the non-breeding season (R'), and the site fidelity rate (F). Other values: (g) groups, hatched on either natural or engineered sandbar, (yr) year-specific variation, (a1) first year different than adult, (A) age-at-banding, (H) hatch date (standardized to June 1st), (D_{NEST}) nesting density, (D_{FOR}) foraging density, and (ca) common adult value among groups.

^B Minimum QAIC_c = 1283.941, c-hat = 1.027

Table 9: Monte Carlo estimates from model-averaged parameter estimates and unconditional standard errors from the Barker (1997) model for piping plovers banded as chicks (N = 685) on the Gavins Point Reach of the Missouri River and Lewis and Clark Lake from 2005 – 2008.

Parameter ^A	Period	Estimate ^B	Standard Error	Lower 95% Confidence Limit	Upper 95% Confidence Limit
S _{adult, engineered}	2006 – 2007	0.793	0.078	0.602	0.907
S _{adult, natural}	2006 – 2007	0.764	0.215	0.239	0.971
p _{chick, engineered}	2005 – 2007	0.777	0.074	0.601	0.890
p _{chick, natural}	2005 – 2007	0.531	0.120	0.305	0.745
p _{adult, all}	2006 – 2007	0.890	0.074	0.650	0.972
R _{chick, all}	2005 – 2007	0.146	0.028	0.010	0.210
R _{adult, engineered}	2006 – 2007	0.263	0.049	0.178	0.369
R _{adult, natural}	2006 – 2007	0.128	0.067	0.044	0.321
R' _{all}	2005 – 2007	0.000	0.000	0.000	0.749
F _{adult, engineered}	2006 – 2007	0.792	0.093	0.557	0.920
F _{adult, natural}	2006 – 2007	0.716	0.305	0.118	0.979
β _{hatch date}		-0.087	0.016	-0.118	-0.057
β _{age at banding}		-0.013	0.072	-0.155	0.128
β _{age at banding*hatch date}		0.005	0.003	-0.001	0.011
β _{natural nesting density}		1.158	0.583	0.017	2.300

β engineered nesting	-0.782	0.198	-1.170	-0.394
density				

^A True survival (S), resight rate on the breeding grounds (p), resight rate during the nonbreeding season (R), the mortality rate of birds that were sighted during the non-breeding season (R'), the site fidelity rate (F), and the effects of individual covariates (β) for first-year (chick) and adult birds hatched on natural or engineered sandbars.

^B Estimates and standard errors for estimates that are not both year- and group-specific were derived from Monte-Carlo procedure with 10000 iterations to combine year- and group-specific estimates.

Table 10: Estimates of true survival for breeding piping plovers.

Study	Estimates (CI ₉₅)	Years	Population
LeDee (2008)	0.91 (0.63 – 0.98)	1998 – 2005	Increasing ^A
This study	0.822 (0.747 – 0.878)	2005 – 2006	Stationary ^C
	0.824 (0.736 – 0.887)	2006 – 2007	
Cohen et al. (2006)	0.714 (0.551 – 0.856)	2002 – 2003	Decreasing ^B
	0.751 (0.527 – 0.891)	2003 – 2004	
	0.643 (0.462 – 0.791)	2004 – 2005	

^A Haig et al. (2005)

^B Cohen et al., in press

^C G. Pavelka, USACE, personal communication

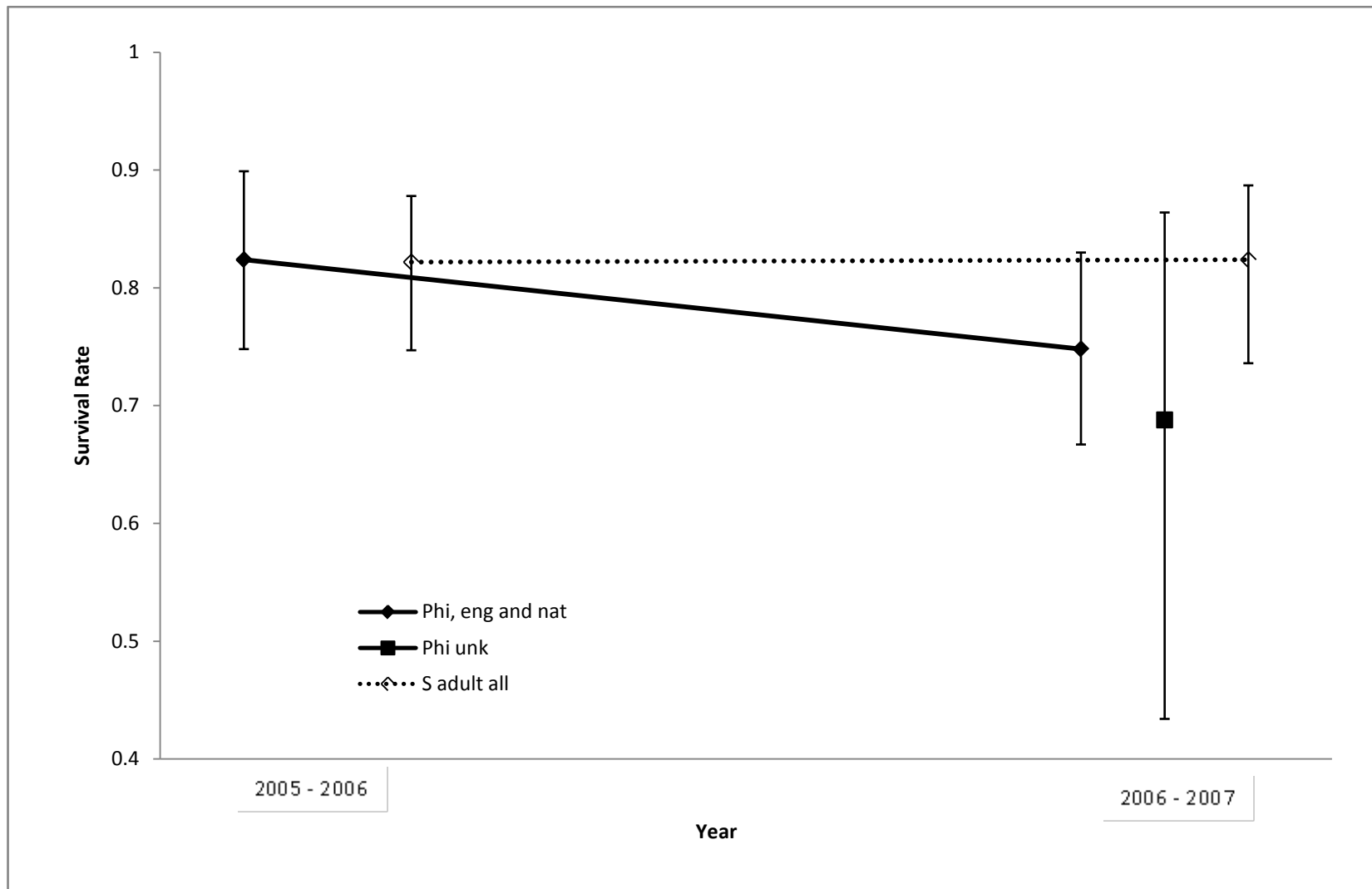


Figure 1: Apparent (Phi) and true survival (S) estimates for piping plovers captured as adults on the Gavins Point Reach of the Missouri River and Lewis and Clark Lake from 2005 – 2007. Error bars represent 95% CIs.

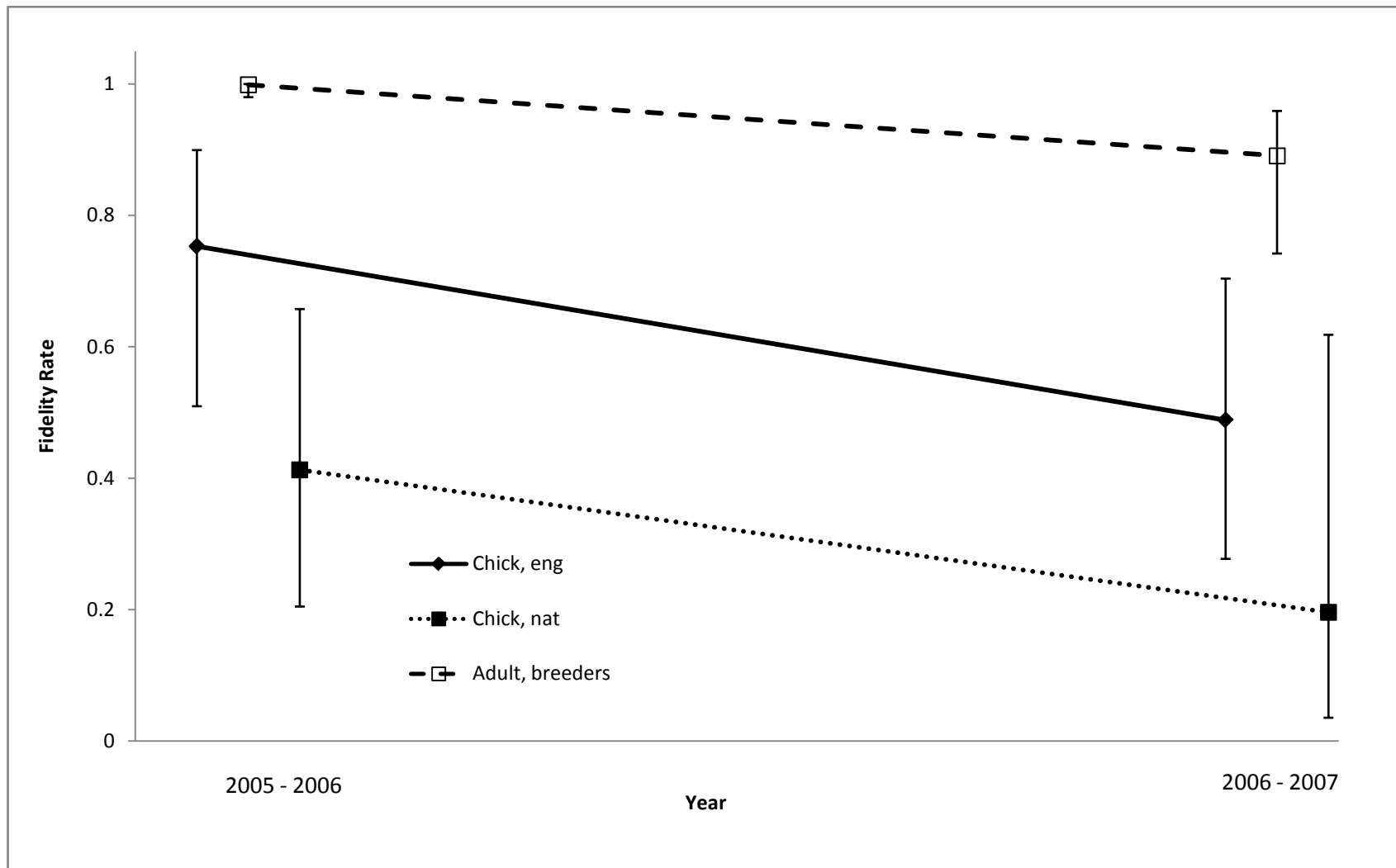


Figure 2: Site fidelity of piping plovers banded as adults and as chicks to the Gavins Point Reach of the Missouri River and Lewis and Clark Lake from 2005 – 2007. Bars represent 95% CIs.

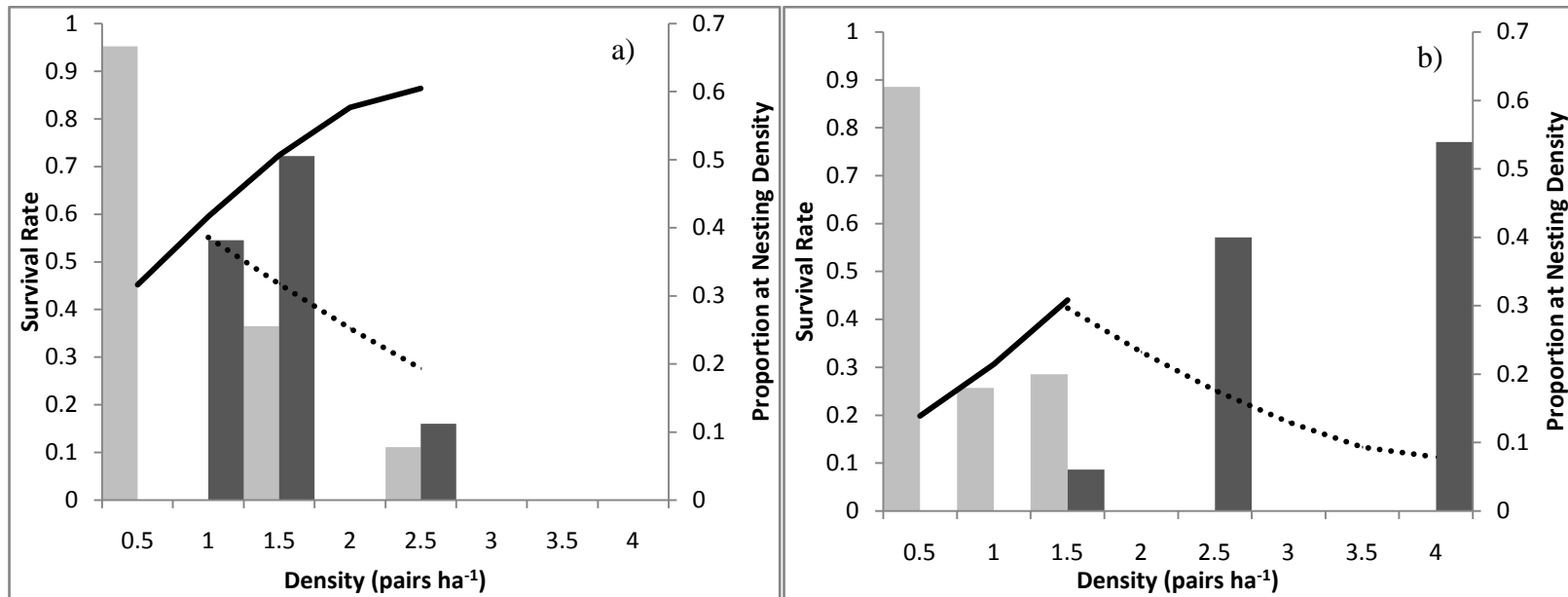


Figure 3: The relationship between juvenile survival and nesting densities on the Gavins Point Reach of the Missouri River and Lewis and Clark Lake from a) 2005 – 2006 and b) 2006 – 2007. The values for age at banding (2.6 days) and hatch date (25 days since 1-Jun) were held constant at the average for all chicks. Lines represent estimated survival rate over the range of observed densities for natural sandbars (solid line) and engineered sandbars (dotted line). The columns represent the proportion of chicks at each density for natural sandbars (light shading) and engineered sandbars (dark shading).

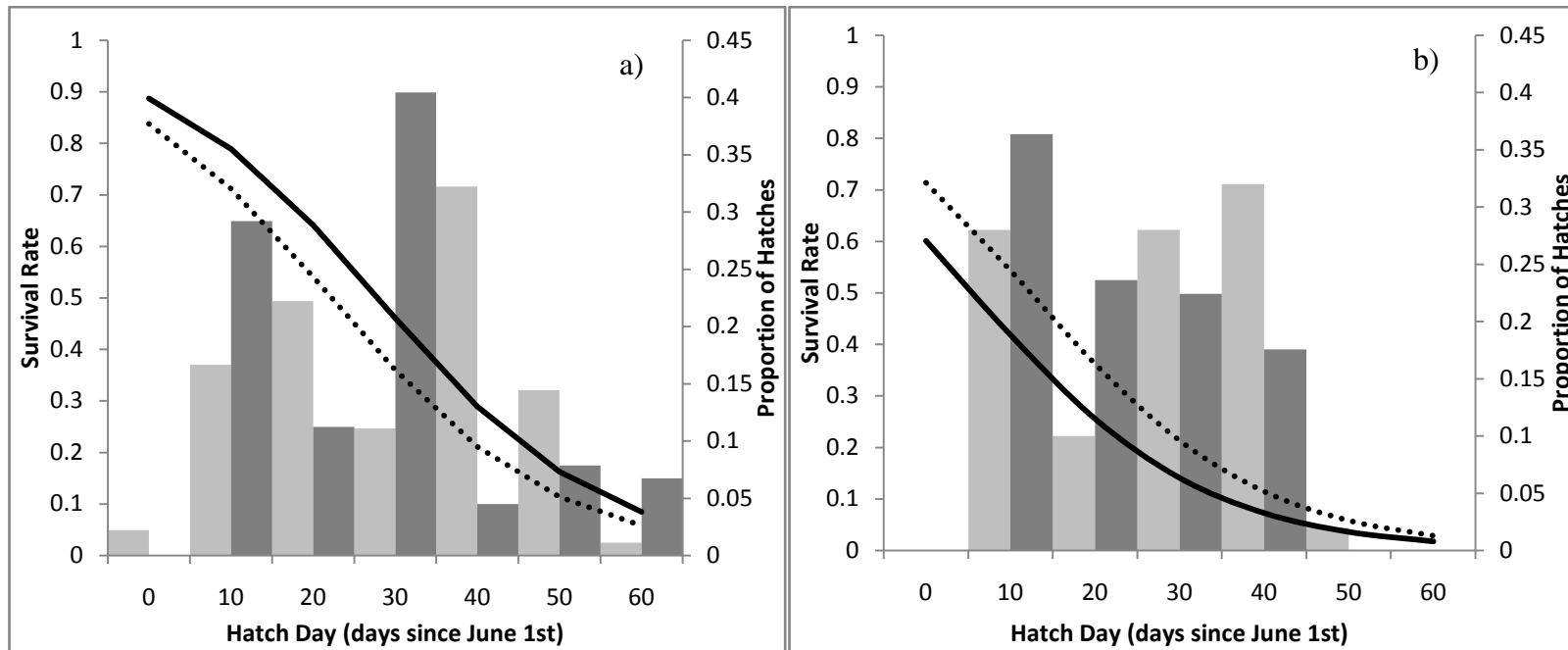


Figure 4: The relationship between juvenile survival and hatch dates on the Gavins Point Reach of the Missouri River and Lewis and Clark Lake from a) 2005 – 2006 and b) 2006 – 2007. The values for age at banding (2.6 days) and nesting density [natural sandbars: a) 0.8 pairs ha^{-1} , b) 0.5 pairs ha^{-1} ; engineered sandbars a) 1.5 pairs ha^{-1} , b) 2.3 pairs ha^{-1}] were held constant at the average for all chicks. Lines represent estimated survival rate for natural sandbars (solid line) and engineered sandbars (dotted line). The columns represent the proportion of chicks at each hatch date for natural sandbars (light shading) and engineered sandbars (dark shading).

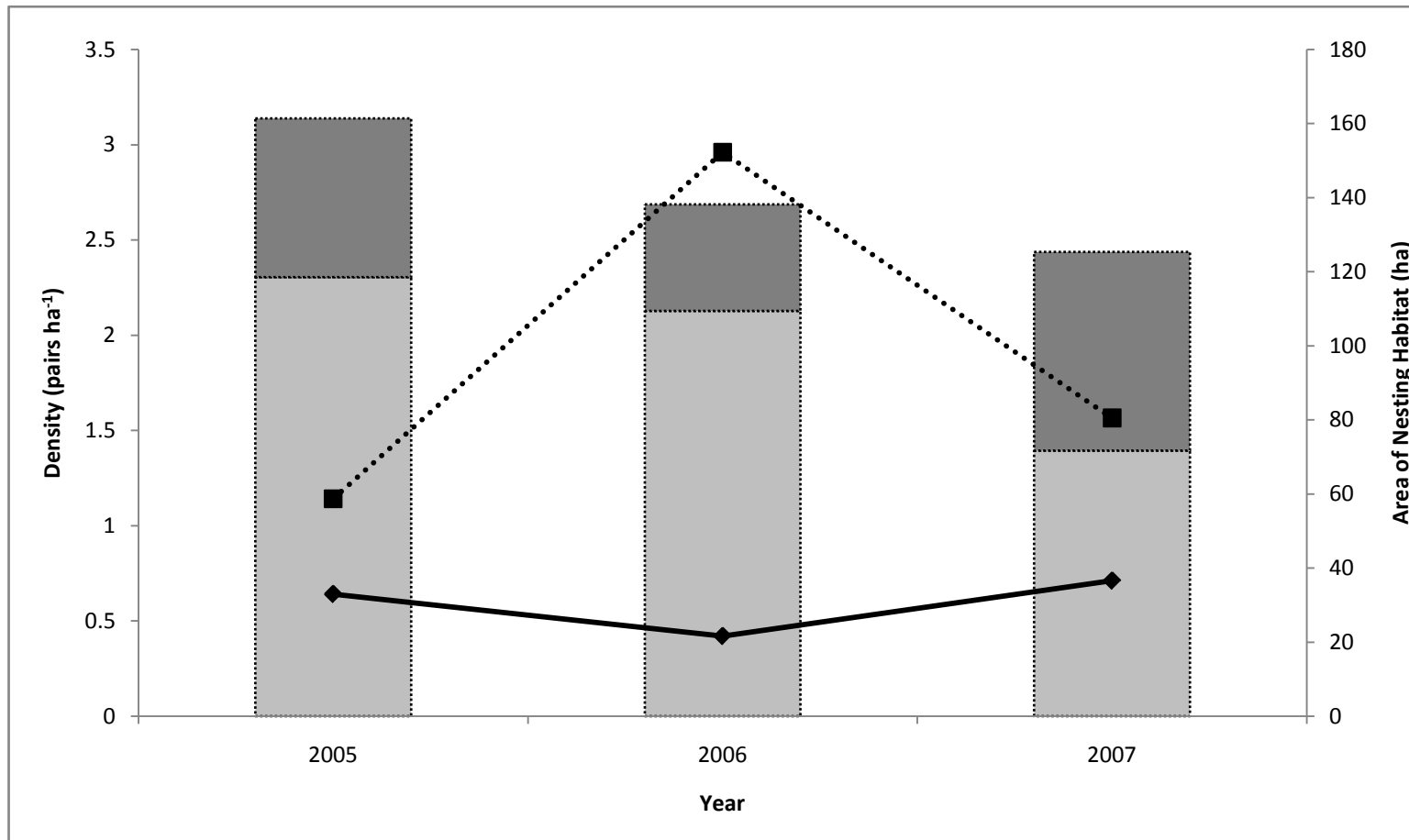


Figure 5: Nesting density of piping plovers using engineered and natural sandbars and nesting habitat availability on the Gavins Point Reach of the Missouri River and Lewis and Clark Lake from 2005 – 2008. Lines represent the estimated density for natural sandbars (solid line) and engineered sandbars (dotted line). Columns represent the amount of nesting habitat available on natural sandbars (light shading) and engineered sandbars (dark shading).

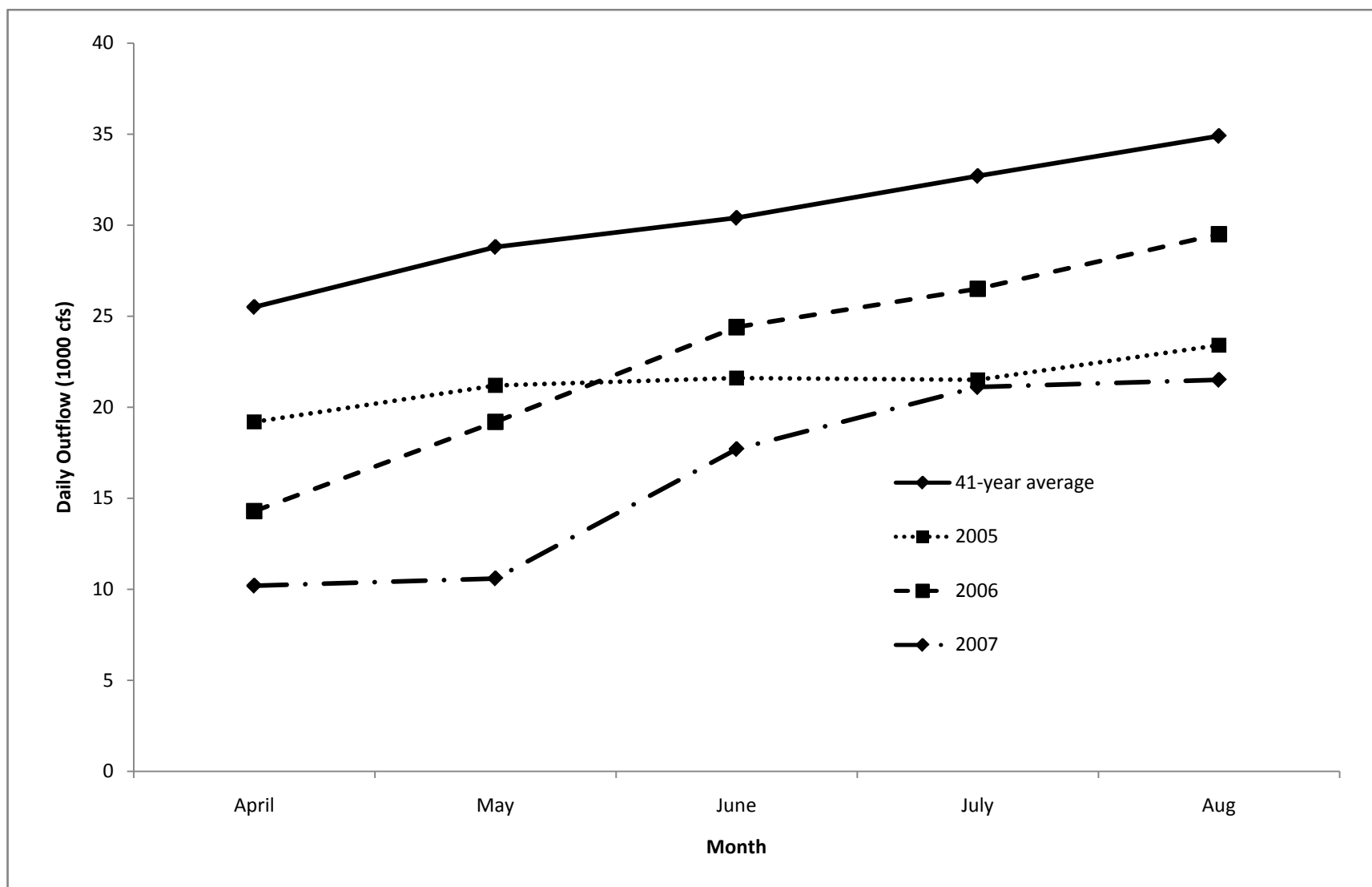


Figure 6: Average daily outflow from the Gavins Point Dam during the piping plover breeding season.

Chapter 3: Potential Piping Plover Population Growth Rates under Observed Demographic Parameters

Potential Piping Plover Population Growth Rates under Observed Demographic Parameters

Daniel H. Catlin, Joy H. Felio, James D. Fraser, and Jonathan B. Cohen

Department of Fisheries and Wildlife Sciences, 100 Cheatham Hall, Virginia Polytechnic Institute and State University, Blacksburg, VA, 24061

Abstract

Habitat limitation and predation regulate many shorebird populations. We studied the effects of habitat creation on a population of the threatened piping plovers (*Chardrius melodus*) nesting on Missouri River sandbars. We used parameter estimates (adult survival, survival from hatch to recruitment, within-population movement rates, and percent of juveniles breeding) derived from data collected from this study and an estimate of renesting rate from the literature and calculated the population growth rate (λ) under several scenarios. In addition, we conducted a sensitivity and elasticity analysis to determine which vital rates make the greatest contribution to the population growth rate. The average parameter estimates predicted positive population growth, estimates from a year of low reproduction and low apparent survival (2006 – 2007) resulted in a predicted negative population growth. Sensitivity and elasticity analyses indicated that adult apparent survival, particularly on engineered sandbars, had the greatest effect on population growth, highlighting the importance of engineered sandbars and adult movement to population growth. Our results suggest that there were short-term successes related to created habitat, but the most recent parameter estimates (2006 – 2007) indicate that engineered habitat may require significant monitoring and management to remain useful.

Keywords: Population growth, engineered habitat, Missouri River, shorebirds

Introduction

Predation and habitat loss have contributed to the decline of many shorebird populations (Dowding and Murphy 2001, Morrison et al. 2001, Nebel et al. 2008). Although reduction of habitat loss is often preferable, certain situations necessitate the creation of habitat or restoration of degraded habitat. The use of human-created habitat, particularly by seabirds and species with similar habitat needs (sandy habitat with little or no vegetation), is well documented (Krogh and Sweitzer 1999, Mallach and Leberg 1999, Collis et al. 2001, Erwin 2002, Erwin et al. 2003, Erwin and Beck 2007, Spear et al. 2007, Jenniges and Plettner 2008). These habitats, however,

may require continual management of both vegetation (Erwin et al. 2003, Spear et al. 2007) and predators (Erwin et al. 2003, Erwin and Beck 2007). Although bird responses to such habitat have largely been positive, work is needed to determine the long-term effects of habitat creation and management on population dynamics (Erwin 2002), particularly in light of the continual management that often is required (Scott et al. 2005).

Piping plovers (*Charadrius melodus*) on the Missouri River nest primarily on the ground on sparsely vegetated sandbars and lakeshores (Prindiville Gaines and Ryan 1988, Espie et al. 1996) and appear to be limited by habitat loss and degradation and predation of nests and young (USFWS 2003). Before human intervention, sandbars were deposited and vegetation was scoured by high flows. In the mid-20th century, multiple dams were built that impounded a large proportion of the mainstem of the Missouri River. Decreased flows caused by these dams have hindered the creation of new sandbar habitat, and existing habitat has been lost through erosion or has become less suitable through vegetation encroachment (USFWS 2003).

The U.S. Army Corps of Engineers (USACE) management of the piping plover on the Missouri River is aimed at increasing reproductive output. Techniques used include symbolic fencing (stakes, twine, and informational signs to reduce human disturbance), nest exclosures (small cages to deter nest predators), predator control (predator trapping and removal to reduce predation on nests, chicks, and adults), and habitat creation and modification programs (creation of new sandbars and vegetation removal from existing sandbars). We studied the population response of piping plovers to habitat creation by estimating demographic parameters under various treatments (Chapters 1 and 2). Here we use those estimated parameter values in a metapopulation model, to explore the possible effects of habitat creation on population growth.

Methods

Study Area

We studied piping plovers on the stretch of the Missouri National Recreational River below the Gavins Point Dam (ca. 95 km of river) in 2005-2007 and included a newly created engineered sandbar on Lewis and Clark Lake (the Lake) in 2007. The Gavins Reach is one of the last free-flowing, unchannelized portions of the Missouri River, and piping plover habitat consists of sandbars that are largely unconnected to the shore. Much of the habitat available for nesting piping plovers consisted of sand deposited during relatively high flows in the late 1990s (USFWS 2003). Existing natural sandbar habitat varied widely in size and composition, from

low unvegetated mud and sandflats, to higher sandbars with stands of cottonwood (*Populus* sp.) and willow (*Salix* sp.) saplings (LeFer 2005). Through the breeding season, herbaceous plants grew along the shorelines of most sandbars (LeFer 2005). In 2004, three sandbar complexes (2 or more sandbars separated by relatively shallow channels) were created to augment current habitat. The USACE created these sandbars through a mixture of dredging and other mechanical methods (such as moving sediment with a bulldozer). In general, the engineered sandbars were longer than wide (in the direction of river flow), and in 2005, the three sandbars were 6.78, 20.58, and 20.71 ha, respectively. In 2007, a sandbar complex was created within the upper portion of the Lake (ca. 27 km from the Gavins Point Reach and ca. 37 km from the nearest river sandbar in this study), and this complex was added to the research area for this study. The 2 sandbars in this complex were less elongate than those built in the river and totaled 27.3 ha during the 2007 breeding season. The study included 12 natural sandbar complexes and 4 engineered sandbar complexes.

Basic Matrix Models

We developed a stage- and female-based, deterministic matrix metapopulation model to calculate the population growth rate. For the most basic model, we modeled separate dynamics for birds breeding on engineered sandbars and those breeding on natural sandbars. The disconnected metapopulation model (*Model 1*) assumed no movement between the two subpopulations and is shown below for engineered sandbars. We used the same structure for natural sandbars:

$$\begin{bmatrix} F_{E,J} & F_{E,A} \\ S_{E,A} & S_{E,A} \end{bmatrix} \quad (1)$$

$$F_{E,A} = ([N_{E,A}CS_{NEST}] + [N_{E,A}C(1 - S_{NEST})RS_{NEST}] + [N_{E,A}C((1 - S_{NEST})R)^2S_{NEST}] + [N_{E,A}C((1 - S_{NEST})R)^3S_{NEST}])S_{E,H} \quad (2)$$

$$F_{E,J} = (P_{BREED}\{[N_{E,A}CS_{NEST}] + [N_{E,A}C(1 - S_{NEST})RS_{NEST}] + [N_{E,A}C((1 - S_{NEST})R)^2S_{NEST}] + [N_{E,A}C((1 - S_{NEST})R)^3S_{NEST}]\})S_{E,H} \quad (3)$$

The definitions of the parameters and subscripts for the models are provided in Table 1. We further developed this basic model, by adding estimates of movement between the two subpopulations (*Model 2*).

$$\begin{bmatrix} F_{N,J}(1 - M_{NE,J}) & F_{E,J}(M_{EN,J}) & F_{N,A}(1 - M_{NE,J}) & F_{E,A}(M_{EN,J}) \\ F_{N,J}(M_{NE,J}) & F_{E,J}(1 - M_{EN,J}) & F_{N,A}(M_{NE,J}) & F_{E,A}(1 - M_{EN,J}) \\ S_A(1 - M_{NE,A}) & S_A(M_{EN,A}) & S_A(1 - M_{NE,A}) & S_A(M_{EN,A}) \\ S_A(M_{NE,A}) & S_A(1 - M_{EN,A}) & S_A(M_{NE,A}) & S_A(1 - M_{EN,A}) \end{bmatrix} \quad (4)$$

Most of the estimates that we used as input in the model were obtained from a field study of piping plover population dynamics on the Gavins Point Reach and Lewis and Clark Lake on the Missouri River from 2005 – 2008 (Table 2). We did not have reliable estimates of reneesting rate from our data, so we used an estimate from a 12-year study of piping plovers on the Atlantic Coast, where individual pairs were monitored more closely (Cohen et al., in press).

We had two, year-specific estimates of adult apparent survival, hatchling apparent survival, and hatchling movement rate from engineered to natural sandbars (2005 – 2006 and 2006 – 2007; Table 2; Chapter 2). Apparent survival is a function of true survival and permanent emigration from the study area (Sandercock 2006). The parameter estimates from 2005 – 2006 indicated relatively high reproductive output (hatchling survival and site fidelity were high) and relatively high adult apparent survival (high adult site fidelity), whereas the parameter estimates from 2006 – 2007 comprised relatively low reproductive output (hatchling survival and site fidelity were low) and relatively low adult apparent survival (low adult site fidelity; Chapter 2).

In our modeling efforts, we estimated the population growth rate if “average conditions” prevailed, if “good” conditions prevailed, and if “bad” conditions prevailed. For average conditions, we averaged the year-specific estimates of 2005 – 2006 with those from 2006 – 2007. We referred to the model that used both years’ parameter estimates as the “average reproduction, average survival” model (*Model 2*). For the “good conditions” case, we used only the estimates from 2005 – 2006 and refer to this as the “high reproduction, high survival” scenario (*Model 3*). For the “bad conditions” case, we used the values obtained in 2006 – 2007 and refer to this as the “low reproduction, low survival” scenario (*Model 4*).

For each scenario, we calculated the finite growth parameter (the population size in year $N+1$ divided by the population size in year N , λ), and we calculated sensitivity and elasticity for each of the elements in the matrix for model 2. Sensitivity and elasticity are measures of how important population parameters are to the growth rate (λ) of the population under consideration (Caswell 2001). Specifically, sensitivity evaluates the effects of small changes in the input parameters on λ , and elasticity is a sensitivity measure that is proportional to both λ and the input parameter (Mills and Lindberg 2002). For both sensitivity and elasticity, life-history parameters with higher values of sensitivity and elasticity have a greater effect on the population growth rate than those with lower values.

Results

The basic metapopulation model indicated that the Gavins Point Reach piping plover population was growing approximately 2% each year (Table 3, Model 2). When we modeled the two subpopulations (natural and engineered sandbars) as separate, the growth rate was positive (+3%) for engineered sandbars and negative (-1%) for natural sandbars (Table 3, Model 1).

The high reproduction, high survival scenario increased the estimate of lambda from the baseline model by 0.13 (Table 3, Model 3), and the growth estimate from the low reproduction, low survival scenario was 0.13 less than the baseline model (Table 3, Model 4).

The parameters associated with adult fecundity, survival, and movement on engineered sandbars had the highest sensitivity values (0.4255, 0.4946, 0.4411, 0.5160), followed by those of adults on natural sandbars (0.2506, 0.2913, 0.2598, 0.3039).

$$Sensitivity = \begin{bmatrix} 0.0934 & 0.1125 & 0.2506 & 0.4255 \\ 0.1086 & 0.1308 & 0.2913 & 0.4946 \\ 0.0968 & 0.1167 & 0.2598 & 0.4411 \\ 0.1133 & 0.1365 & 0.3039 & 0.5160 \end{bmatrix} \quad (5)$$

The sensitivity values in Eqn. 5 refer to the corresponding matrix elements in Eqn. 4.

Adult survival and site fidelity on engineered sandbars had the largest elasticity value (0.3595), followed by adult survival and site fidelity on natural sandbars (0.1609).

$$Elasticity = \begin{bmatrix} 0.0140 & 0.0061 & 0.0452 & 0.0280 \\ 0.0028 & 0.0214 & 0.0089 & 0.0977 \\ 0.0600 & 0.0081 & 0.1609 & 0.0308 \\ 0.0167 & 0.0951 & 0.0447 & 0.3595 \end{bmatrix} \quad (6)$$

The elasticity values in Eqn. 6 refer to the corresponding matrix elements in Eqn. 4.

Discussion

Habitat Creation

The use of engineered sandbars, islands, and other human created habitats is well established (Krogh and Schweitzer 1999, Mallach and Leberg 1999, Erwin et al. 2003, Erwin and Beck 2007, Spear et al. 2007, Jenniges and Plettner 2008). However, use does not, in itself, indicate a positive effect on population dynamics, and more specific information is needed to evaluate these habitats (Erwin 2002). Our model allowed us to investigate not only how patterns of habitat use affected population growth, but also how the two habitat types interacted. The creation of engineered habitat appeared to have a positive effect on population growth. When engineered and natural habitats were modeled together, the population exhibited positive growth, but when modeled separately, the growth rate for natural sandbars was negative and the growth

rate for engineered sandbars was positive, suggesting that the positive effects of engineered habitat were over-riding the negative effects of natural sandbar habitat. Moreover, the sensitivity values for adults on engineered habitat were the highest, and the elasticity value for survival and movement of adults on engineered habitat was higher than that for adult survival and movement on natural habitat, indicating that adults on engineered habitat made a greater contribution to the population growth rate than adults on natural sandbars. Since the adult survival rate was identical on engineered and natural habitats, the importance of adults on engineered habitat must have been driven by relatively lower emigration rates and relatively higher fecundity rates than those on natural sandbars. Unfortunately, our estimates of hatchling survival and juvenile recruitment do not include years prior to the creation of sandbar habitat, so we cannot evaluate if the predicted negative population growth on natural sandbars was evident before the creation of habitat or was linked to sandbar creation, perhaps by enticing birds to move from natural to engineered habitat.

Despite the positive effect of engineered habitat, the modeling using the most recent year of data, 2006 – 2007, the low reproduction, low survival scenario, predicted negative growth despite the presence of engineered habitat, indicating that further research is needed to understand the ultimate effects of engineered habitat. Based on sensitivity and elasticity values, the relatively low apparent adult survival in 2006 – 2007 (as a result of low site fidelity) probably made the greatest contribution to the negative predicted population growth. It is possible that habitat creation, in the absence of other management, will only create a temporary 1 – 2 year increase in population growth or that the amount of engineered habitat created was insufficient to sustain population growth. Alternatively, it is possible that unmeasured but temporary factors created the low parameter values in the final year of the study.

In general, the sensitivity and elasticity analyses indicated that adult survival was the most important factor determining population growth, which is similar to other studies (Ryan et al. 1993, Plissner and Haig 2000, Larson et al. 2002, McGowan 2008). For a species with a relatively high survival rate that breeds in disturbed habitats, it stands to reason that adult survival has a greater effect on population growth than fecundity, particularly on the Missouri River where periodic floods would have greatly reduced fecundity. Although it often is difficult to manage for adult survival, we found that lower apparent survival was a function of low site fidelity, and not mortality. If one has local goals for population growth, one may manage for

reduced emigration either through habitat creation or increasing of reproductive success, thus effectively managing for high adult apparent survival.

Future Modeling

The development of a more explicit model would allow us to investigate other features of the system and to evaluate more specific hypotheses about the effects of management. In particular, the creation of a spatially-explicit metapopulation model would allow us to model dispersal as a function of distance and location. The connection between natural and engineered sandbars had a substantial effect on the finite population growth of individuals using natural habitat, so it is possible that a more explicit model of dispersal would give us insight into how these dynamics are operating. The addition of some density dependence in the model also would make the exercise more realistic. Often the nature of density-dependence is unknown (Larson et al. 2002, McGowan 2008), but we are beginning to understand the effects of density on several of the plover population dynamics parameters (Chapter 2). We have a model for the effect of density on hatchling survival and movement, and in a spatially-explicit model we could implement these factors. Additionally, some information about the availability of habitat as well as the carrying capacity of that habitat would greatly improve this model. Ultimately, the extension of our research beyond the Gavins Point Reach, would offer the opportunity to model a larger portion of the Great Plains population in a manner similar to what we have done with the Gavins Point Reach. There is connection among the nearby subpopulations and the regional population (Chapter 2), and by further developing this model, we could begin to make informed predictions about when and where management is most needed throughout a greater region.

Conclusion

Our results suggest that engineered habitat has the potential to mitigate the effects of habitat loss and degradation. However, the low reproductive output in 2006 and low apparent adult survival (influenced by high adult emigration) from 2006 to 2007 suggest that insufficient habitat creation, or water management that contributes to high plover densities and/or low reproductive output, or excessive predation, or all of these factors jointly, can result in a decreasing plover population.

It is unclear whether the habitat creation program is sustainable in the long-term. The creation of sandbar habitat is expensive, and there is mounting evidence that densities and predation on these habitats increase quickly (Chapter 2), potentially creating habitat sinks

(habitats that require constant immigration to maintain a population). The maintenance of these habitats as sources (habitats that produce enough, or more than enough recruits for a stationary population) may require continual removal of predators and vegetation, continued creation of sandbars, and potentially modification of flow regimes to control habitat availability and nesting densities.

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Table 1: Code definitions for parameters and subscripts used in the metapopulation matrix model for piping plovers nesting on the Gavins Point Reach and Lewis and Clark Lake on the Missouri River

Type	Code	Definition
Parameter	N	Breeding population size
	S	Apparent Survival Rate
	F	Fecundity (Female juvenile recruits /female)
	C	Clutch Size
	R	Renest rate
	M	Movement rate
Subscript	E	Engineered sandbars
	N	Natural sandbars
	A	Adult
	H	Hatchling
	J	Juvenile
	Nest	Nest estimate

Table 2: Input values for the stage- and female-based, deterministic metapopulation matrix model for piping plovers nesting on the Gavins Point Reach and Lewis and Clark Lake on the Missouri River.

Parameter	Estimate	Source
Clutch size (females only), C	2	constant
Nesting success, S_{NEST}	0.491	Chapter 1
Renest rate, R	0.520	Cohen et al., in press
Breeding probability for juveniles, P_{BREED}	0.830	Chapter 2
Adult movement, engineered to natural sandbar, $M_{EN,A}$	0.091	Chapter 2
Adult movement, natural to engineered sandbar, $M_{NE,A}$	0.192	Chapter 2
Hatchling movement, engineered to natural sandbar, $M_{EN,H}$	0.196 ^a 0.304	Chapter 2
Hatchling movement, natural to engineered sandbar, $M_{NE,H}$	0.145	Chapter 2
Annual adult survival, S_A	0.827 ^a 0.735	Chapter 2
Annual hatchling survival, engineered sandbars, $S_{E,H}$	0.270 ^a 0.134	Chapter 2
Annual hatchling survival, natural sandbars, $S_{N,H}$	0.219 ^a 0.105	Chapter 2

^a Parameters with two values represent year-specific estimates. .

Table 3: Piping plover finite population growth rate (λ) from a deterministic matrix metapopulation model. Input parameter values are from estimates from the Gavins Point Reach and Lewis and Clark Lake on the Missouri River from 2005 – 2008. Lambda was estimated by calculating the dominant eigenvalue of each of the matrices. When $\lambda = 1$ the population is stationary, $\lambda > 1$ the population is increasing, and $\lambda < 1$ the population is decreasing.

Model	Model Scenario	$\lambda_{\text{Engineered}}$	λ_{Natural}	λ_{Total}
1	Disconnected ^a average reproduction, average survival ^b	1.04	0.99	
2	Average reproduction, average survival ^b			1.02
3	High reproduction, high survival ^c			1.15
4	Low reproduction, low survival ^d			0.89

^a Scenario where the dispersal between engineered sandbars and natural sandbars and the converse is fixed at zero.

^b Hatchling survival (reproduction) and adult survival (survival) estimates from both years of the study.

^c Hatchling survival (reproduction) and adult survival (survival) estimates from 2005 – 2006.

^d Hatchling survival (reproduction) and adult survival (survival) estimates from 2006 – 2007.

CONCLUSION

Overall, engineered habitat appeared to provide a suitable substitute for naturally created habitat. Piping plovers nested on engineered habitat more than would be expected by its availability, and the nesting success of individuals on engineered sandbars was higher than that of individuals on natural habitats after controlling for enclosure effects. The survival of adult plovers on engineered habitat was similar to that of adults on natural habitat. Furthermore, the presence of engineered habitat appeared to contribute to the predicted positive growth of the Gavins Point Reach population, as compared to the scenario where engineered and natural habitats were disconnected. The values of demographic parameters of the population nesting on natural habitat prior to the creation of habitat are unknown, so we are unable to predict what may have happened to the population in the absence of the habitat creation effort. The Gavins Point population had grown steadily since 1997, but was leveling off prior to and immediately after the creation of new habitat. However, the population growth rate on natural sandbars under the scenario with average reproduction and average survival does appear to be dependent on emigration from engineered sandbars.

Some of the results of our study suggest that we should interpret these short-term successes with caution. We found a negative correlation between juvenile survival and nesting density, and the nesting densities on engineered sandbars did not quickly decrease after the initial population buildup. Engineered sandbars in general had greater nesting densities than natural sandbars as a result of selection for this habitat by adult plovers. If the nesting densities on engineered habitat remain disproportionately high and colonizers do not abandon these habitats as a result of low reproductive success, engineered habitat may begin to act as an ecological trap, such that the habitat attracts individuals but has relatively low reproductive output. The estimated population growth rate based on modeling varied depending on which year's data were used, and the most recent estimates predicted a -11% growth rate. Preliminary results from an analysis of pre-fledging survival in 2007 suggested that survival on engineered habitats continued to decline, but another year of resighting data is needed to determine whether this decreased survival will affect recruitment, constituting a declining trend in the efficacy of engineered habitat. An alternative possibility is that the population on engineered habitats will decline to more normal densities, and then become stationary at those levels.

The decrease in adult apparent survival in the second year of the study was an effect of reduced site fidelity. This immigration may have been driven by high density, or some experience that resulted from high density, such as increasing altercations with neighbors, or low reproductive success. As with adults, juvenile site fidelity was low when nesting densities were high and reproductive success was low. These results suggest that, to maintain population levels or to promote population growth, efforts may need to be made to improve reproductive success and maintain low nesting densities through habitat creation. Great-horned owl (*Bubo virginianus*) predation appeared to have the greatest negative effect on reproductive success, but severe owl predation on engineered sandbars did not occur immediately after sandbar construction. The predation may have been related to the high nesting density of piping plovers, or, alternatively, it may have been a function of the time it takes resident owls to discover a new food source.

It should not be surprising that avian predators are population limiting factors for this species. Piping plovers evolved nesting in open, largely tree-free areas including barrier islands, prairie potholes and prairie rivers. Stabilization of barrier islands and river banks, changes in fire and grazing regimes, and changes in river flow dynamics have no doubt resulted in far more trees close to piping plover nesting areas than existed prehistorically. These trees support nesting raptors, crows and other bird species that prey on piping plovers and their eggs. These considerations suggest that, barring true ecosystem restoration that restores prairie conditions to and adjacent to the Missouri River, predators will continue to be problematic for nesting plovers.

A second major cause of pre-fledging mortality appeared to be agonistic interactions. If these types of interactions are more likely to occur at higher densities, then the removal of owls could exacerbate the effects of agonism if the density of plover chicks increases. Further information on the behavioral effects of high densities will be available at the end of our current research efforts.

A theme that connects all of our findings is flow regime or water discharge. The “bad” year, 2006, was characterized by the highest water release levels observed during brood rearing during this study. Our observations suggested that there was less moist foraging substrate available to chicks at this time and preliminary analyses (Catlin and Fraser, unpublished data) suggest lower chick growth rate than in other the two years of the study. Moreover, higher water discharge apparently contributed to higher densities that we linked with lower chick survival

(Chapter 2). Because in this single year we had at once very high densities, relatively high water, and high predation, it is difficult to unravel the relative contributions of each factor to low chick survival and high emigration rates. Our working hypothesis is that predation is density dependent at the density levels observed on engineered sandbars in 2006, and that high water discharges contributed to chick mortality and high emigration rates by increasing density, and by decreasing food availability as well as by flooding out some nests and broods. If this hypothesis is correct, then plover conservation could be enhanced by adjusting water releases to provide substantial plover nesting, and especially foraging habitat. More years of study in which densities and water release levels vary will be required to adequately evaluate this hypothesis.

Beyond the question of the effects of density on behavioral interactions, future research should focus on the length of time that engineered habitat has a positive contribution to the population growth of piping plovers, since these sandbars continue to be used as nesting and brood rearing habitat. Moreover, the study needs to be continued so that predictive models of the effects of engineered habitat will have the appropriate level of variation associated with them. Even if we assumed that our estimates did encompass the range of reproductive output and survival rates, we do not have enough information to determine the relative frequencies of the various rates within that range. This study had an effective sample size of 3 – 4 engineered sandbars, and while those sandbars were, on average, as good as, or better than natural sandbars, there was much sandbar-specific variation in all of the vital rates. By coupling longevity and variability information, we should be able to move towards creating a model that predicts the amount and timing of sandbar construction required to meet recovery goals, and an estimate of whether or not these are attainable using engineered habitat.

Lastly, despite the successes of predator management and habitat creation in improving plover population growth, our results and common sense suggest that these activities are only short-term solutions and cannot contribute to true recovery of the piping plover. Under the Endangered Species Act's (ESA) terminology, these actions do not constitute "conservation" because they cannot bring piping plovers "to the point at which the measures provided pursuant to this Act are no longer necessary" (16 USC 1532§ 3 [3]). Regardless of the amount of time engineered habitat will be productive, without continued sandbar creation the system will eventually revert to the conditions that predated listing, and thus, this solution cannot be considered a true conservation action as defined by the ESA. If the ultimate goal is the recovery

of the species such that no further actions under the ESA are necessary, then management activities that are more far-reaching and fundamental need to be implemented.