# INTERIOR LEAST TERN (*STERNULA ANTILLARUM ATHALASSOS*) AND PIPING PLOVER (*CHARADRIUS MELODUS*) NEST SITE SELECTION AT MANAGED, OFF-CHANNEL NESTING SITES ALONG THE CENTRAL PLATTE RIVER, NEBRASKA


PATRICK D. FARRELL

Executive Director's Office for the Platte River Recovery Implementation Program, 4111 4th Avenue, Kearney, NE, 68845

Corresponding Author; E-mail "farrellp@headwaterscorp.com"

DAVID M. BAASCH

Executive Director's Office for the Platte River Recovery Implementation Program, 4111 4th Avenue, Kearney, NE, 68845

JASON M. FARNSWORTH

Executive Director's Office for the Platte River Recovery Implementation Program, 4111 4th Avenue, Kearney, NE, 68845

CHADWIN B. SMITH

Executive Director's Office for the Platte River Recovery Implementation Program, 4111 4th Avenue, Kearney, NE, 68845

**Abstract**.– The Platte River Recovery Implementation Program (Program) and its partners invest substantial resources in creating and managing off-channel nesting habitat for interior least terns (*Sternula antillarum athalassos*) and piping plovers (*Charadrius melodus*) along the central Platte River in Nebraska. One of the management objectives for the Program is to improve productivity of interior least tern and piping plover. We used resource selection functions and 15 years of data to assess the influence physical site attributes and inter- and intra-specific interactions have on nest site selection by interior least terns and piping plovers on off-channel nesting sites. We found nest site selection by interior least terns and piping plovers was influenced by factors the Program can manage such as distance to predator perch and elevation above waterline as well as factors that cannot be managed. We found inter- and intra-specific interactions influenced nest site selection by both species. Being nongregarious, piping plovers avoid nesting in close proximity to each other whereas interior least terns, being colonial, select nest sites in close proximity to each other. We also found probability of interior least tern and piping plover use was maximized when distance to nearest forest was ≥150 m, distance to water was ≥30 m, and elevation above waterline was ≥3 m. As such, habitat management activities implemented at off-channel sites should include the removal of potential predator perches ≤150–200 m from off-channel nesting areas and design plans should attempt to provide maximal amounts of elevated nesting habitat distant to water.

**Key Words**.– Central Platte River, *Charadrius melodus*, interior least tern, nest site selection, off-channel habitat, piping plover, sandpit, *Sternula antillarum athalassos*

**Running Head**.– TERN & PLOVER NEST SITE SELECTION

One of the management objectives for the Platte River Recovery Implementation Program (Program) is to improve productivity of interior least tern (*Sternula antillarum athalassos*, hereafter least tern) and piping plover (*Charadrius melodus*) in the Associated Habitat Reach (AHR; Program 2006). An important consideration for least tern and piping plover productivity within the AHR is nesting and foraging habitat dynamics. Off-channel creation and management strategies have been observed to impact choices of nesting birds. Due to the high incidence of off-channel nesting, it is important to understand how these species are utilizing nest sites created and managed to specifically encourage use by least terns and piping plovers for breeding.

Off-channel nesting habitat has been important for maintaining the presence of both species within the AHR. When regulated by density-dependent factors such as competition, avian species such as piping plovers establish an equilibrium density that is determined by habitat availability associated with territoriality (Fretwell and Lucas 1970, Newton 1992, Rodenhouse et al. 1997, Cohen et al. 2007). Therefore, the Program has focused management activities on restoring, constructing and managing off-channel nesting areas (sandpits) to increase habitat availability and thereby decrease the density of least tern and piping plover breeding pairs within the AHR. The Program and its partners implement management strategies such as providing dry sand areas for nesting during times of high water, removal of woody vegetation ≤60 meters from the nesting areas, constructing water barrier ≥15 meters around nesting areas, chemical application to remove and prevent vegetation establishment, and reducing predation through predator trapping and fencing at all sites. All of these management activities have increased the amount and suitability of nesting habitat during 2009–2015 (Cahis and Baasch 2016). In response to these management actions, the numbers of breeding pairs and productivity of least terns and piping plovers has increased, which supports previous accounts of density dependence in avian and other species (Baasch et al. 2015, Cahis and Baasch 2016).

Predation has been attributed to a majority of chick losses on off-channel sites in the lower Platte River (Kirsch 1996). As such, nesting on artificial sites generally occurs in managed areas where predation has been reduced through trapping, installation of predator fencing, and reducing habitat for predators through mechanical activities such as tree clearing. Thus, we assumed close proximity to wooded areas used by mammalian and avian predators would increase predation potential and thus least terns and piping plovers would select nest sites away from wooded areas. Though off-channel sites are not subject to many of the high water events observed with in-channel nests, based on life history strategies we assumed least terns would be more apt to select for higher elevations than piping plovers (Faanes 1983, Burger 1987). Proximity to water at a nesting location can be especially important for foraging by piping plovers (Elliott-Smith and Haig 2004). Therefore, we assumed piping plover nests would be closer to the edge of water to provide easier foraging opportunities during the breeding season and thus elevations would be slightly lower.

Piping plovers defend territories around nest locations, preventing other piping plovers and possibly least terns from nesting near them (Cairns 1982, Burger 1987). We hypothesized territoriality of piping plover would influence nest site selection and densities of nests in AHR due to constrained habitat availability (Faanes 1983). Least terns, however, are a colonial species that nest near one another and defend nests and chicks by mobbing predators which decreases the probability of predators targeting individual nests (Darling 1938, Burger 1988). Nest site locations may be heavily dependent on the distribution of the first few least tern nests established at an off-channel site. We assumed least tern and piping plover would select off-channel nest site locations in a similar manner based on nest site features, but would differed due to inter- and intra-specific influences (Thompson et al. 1997, Maxson 2000, Elliott-Smith and Haig 2004).

We used resource selection functions (RSFs) to assess the influence physical site attributes and inter- and intra-specific interactions have on nest site selection by least terns and piping plovers. It is assumed that a species will select the best resources available for survival and reproduction and use the better resources disproportionally to their availability (Manly et al. 2007). Resource selection in this study refers to the resources associated with a nest site compared to resources accessible at available locations within the nesting area. We assumed least terns and piping plovers would select nest sites where resources would maximize their breeding potential and that high quality locations would be selected disproportionally to their availability. The objective of this investigation was to understand how physical attributes and inter- and intra-specific interactions influence nest site selection by least terns and piping plovers on managed off-channel sites within the AHR. Findings from this investigation will provide guidance for management of off-channel sites to increase availability of high quality nesting habitat and to improve overall productivity of least terns and piping plovers in the AHR.

## METHODS

### *Study Area*

The AHR is a 145 km reach extending from Lexington, NE downstream to Chapman, NE and encompasses the central Platte River channel and off-channel habitats (sandpits) within three and one half miles of the river (Fig. 1). Only three managed off-channel nest sites were present in 2001, but accumulation of land increased the quantity of sites to nine by 2013, all of which were maintained through 2015 (Table 1). Among other things, management activities at each of the sites has included predator fencing and trapping, pre-emergent herbicide application, and tree removal.

Predator fencing and trapping have not occurred at Trust Wildrose East. We used the Program minimum habitat criteria to determine the amount of nesting habitat that was available each year and to develop breeding pair density estimates (Program 2012, Baasch et al. 2015).

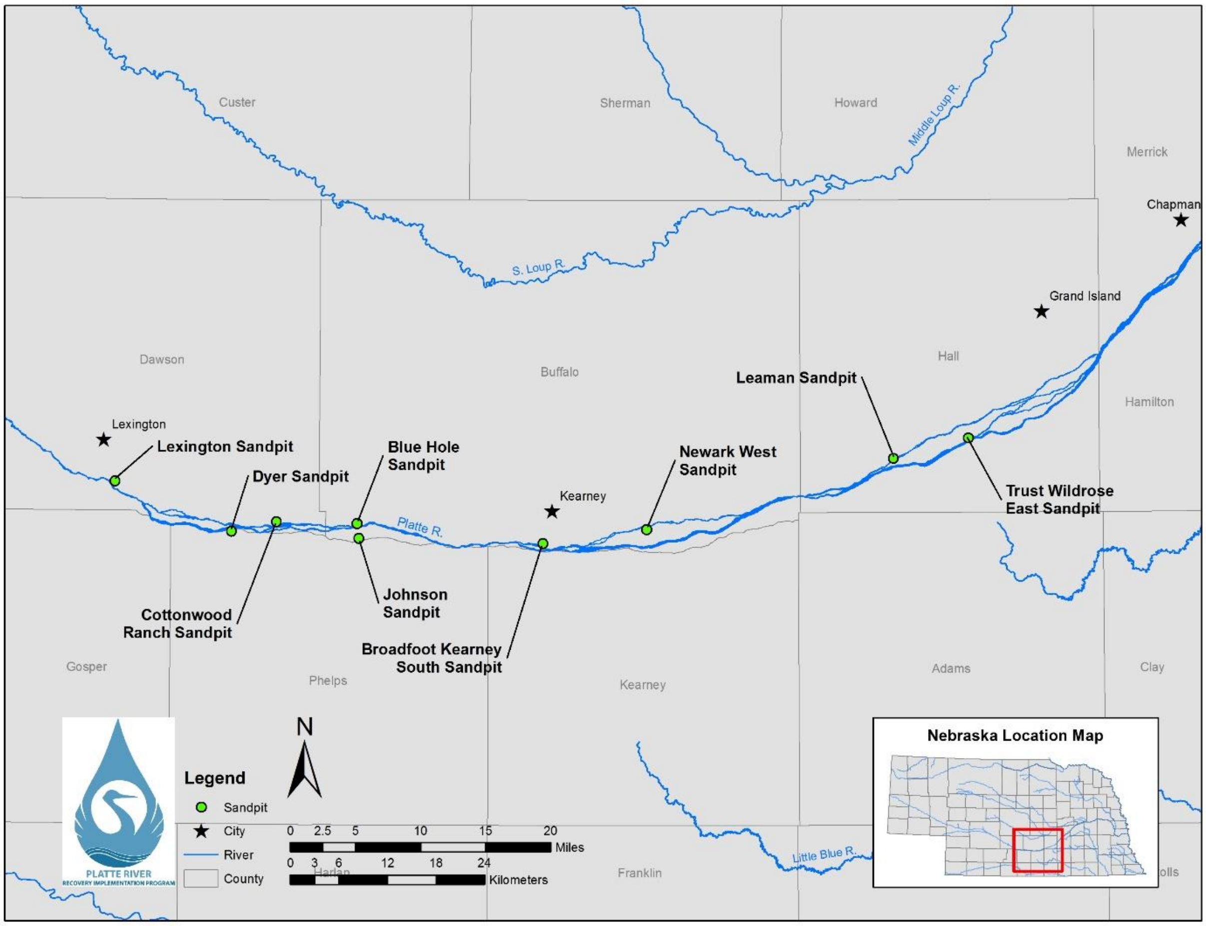



**Figure 1.** Associated Habitat Reach (AHR) of the central Platte River extending from Lexington downstream to Chapman, NE. Nine managed, off-channel nesting sites included in the nest site selection analysis.

**Table 1.** Off-channel nesting sites in the Associated Habitat Reach (AHR) managed for interior least terns (*Sternula antillarum athalassos*) and piping plovers (*Charadrius melodus*). Information presented includes the year sites were first managed, and size of the sites (see Fig. 1).

| Site Name | Year Initiated | Hectares |
|---|---|---|
| Lexington | Prior to 2001 | 6.6 |
| Dyer | 2010 | 8.4 |
| Cottonwood Ranch | 2011 | 6.8 |
| Blue Hole | Prior to 2001 | 10.8 |
| Johnson | Prior to 2001 | 2.0 |
| Broadfoot Kearney South | 2010 | 6.6 |
| Newark West | 2011 | 5.5 |
| Leaman | 2013 | 4.5 |
| Trust Wildrose East | 2008 | 1.1 |

*Least Tern and Piping Plover Nest Location Data*

During nesting seasons of 2001 through 2015, each managed, off-channel nesting site was surveyed at least monthly to document the presence or absence of nesting least terns or piping plovers. Sites where nesting was documented were monitored at least twice per week from late April to early September depending on departure of last fledglings or cessation of nesting or brood-rearing activities. Objectives were to locate and document least tern and piping plover adults, nests, chicks, fledglings, and breeding pairs as well as species productivity. Surveys included documented observations from outside of the habitat area using scopes and binoculars (2001–2015) as well as entering active sites to walk through nesting areas to identify nest locations based on systematic grid searches (2009–2015). Active nests were defined as any scrape containing ≥1 egg. Nests were monitored ≥2 times per week until successful (≥1 chick hatched), failed (evidence of nest destruction or abandonment), or unknown fates (no evidence present) were determined. Due to intense survey effort we assumed the probability of detection was 1.0.

During the initial nest visit we recorded a GPS location for spatial reference, estimated the nest-initiation date by floating eggs, took a photograph of the nest, and collected on site habitat measurements. Habitat measurements collected off-site included elevation above water and distances to nearest waterline, predator perch, and non-suitable habitat.

*Use and Available Location Data Collection*

To populate nest site selection models, we collected physical site attribute and inter- and intra-specific information at each location a nest was found (nest site location) as well as locations within each site that were available for nesting (available locations). We assumed available locations were limited to off-channel sites where nests were found because our investigation is focused on small-scale (within site) as opposed to macro-scale (between site) habitat selection within the AHR. Twenty random points were generated within the off-channel site where each nest was located using the Create Random Points tool in ArcMap. The 20 random points represent a sample of available locations with associated resources and, with the nest site location, make up a “choice set” for each individual nesting event (Cooper and Millspaugh 1999). Choice sets of 20 random points or less were found to be sufficient in other studies (McFadden 1978; Baasch et al. 2009; Unger et al. 2015). Each choice set is unique and linked by a likelihood function to the nest site location using the strata feature in Program R’s gam function (R Core Team 2015).

*Physical Site Characteristics*

We calculated values of attributes hypothesized to influence nest site selection within a site. In an effort to reduce error and maintain consistency, aerial imagery and GPS locations of nests were utilized to determine distance to edge of water (DEW) and distance to predator perch (DPP). All distance measures were collected in ArcGIS (ESRI 2011. ArcGIS Desktop: Release 10. Redlands, CA: Environmental Systems Research Institute). Imagery collected each year was used to quantify DEW, which was defined as the closest Euclidean distance to water from each nest and random location. Given piping plovers forage extensively along the edge of the water, we quantified waterline length (WLL) within a 1.30 ha area (average nesting density) around each piping plover nest. Distance to predator perch was defined as the Euclidean distance to the closest object ≥3 m tall that could be utilized by a predator. LiDAR imagery was used to measure elevation above water (EAW) of off-channel sites. LiDAR images were paired with digital elevation models to produce a spatial surface of nest sites with elevations compared to surrounding water. Nests and random locations were assigned an elevation value based on their location on the nest site.

*Inter- and Intra-Specific Interactions*

We considered both inter- and intra-specific interactions as predictors of nest site selection at managed, off-channel sites. Distance to nearest piping plover nest (PPN) and least tern nest (LTN) were calculated based on GPS locations for each least tern and piping plover nest. We used ArcGIS to identify which least tern and piping plover nest were nearest in proximity to the newly established least tern or piping plover nest. Only least tern and piping plover nests that were established and had not failed or succeeded were considered when determining which nests were closest to the newly initiated nest. Due to the inability of our resource selection function to handle missing data points, if no other least tern or piping plover nest was present at an off-channel site when a least tern or piping plover nest was established, the newly established nest and associated random locations were given a distance measure of 0 m. Nests that were established when no other least tern or piping plover nest was present were removed from the summary statistics.

*A priori Model Set*

We developed *a priori* candidate models, including a null model, to understand how different covariates and combinations of covariates influence off-channel nest site selection (Table 2). We elected to limit the model set in our analysis to the 36 combinations listed in Table 2 as other combinations seemed less plausible based on species' behavior.

**Table 2**. Nest site selection *a priori* model list evaluated for interior least terns (*Sternula antillarum athalassos*) and piping plovers (*Charadrius melodus*).

| Model | Least tern | Piping Plover |
|---|---|---|
| 1 | NULL | NULL |
| 2 | EAW | EAW |
| 3 | DPP | DPP |
| 4 | DEW | DEW |
| 5 | LTN | LTN |
| 6 | PPN | PPN |
| 7 | LTN+PPN | EAW+DPP |
| 8 | EAW+DPP | EAW+DPP+PPN |
| 9 | EAW+DPP+LTN | PPN+DEW |
| 10 | EAW+DPP+LTN+PPN | DPP+PPN |
| 11 | DPP+LTN+PPN | EAW+DPP+DEW |
| 12 | EAW+DPP+DEW | DPP+DEW |
| 13 | EAW+LTN+PPN | EAW+DPP+PPN+LTN |
| 14 | EAW+DPP+PPN+LTN+DEW | EAW+PPN+LTN |
| 15 | - | DPP+PPN+LTN |
| 16 | - | EAW+DPP+PPN+LTN+DEW |
| 17 | - | WLL |
| 18 | - | PPN+WLL |
| 19 | - | EAW+DPP+WLL |
| 20 | - | DPP+WLL |
| 21 | - | WLL+PPN+ LTN |
| 22 | - | EAW+DPP+PPN+LTN+WLL |

*Statistical Analysis*

We utilized general additive models (GAMs) within a discrete choice model (DCM) framework for training datasets of least tern and piping plover off-channel nest site selection from 2001 to 2015. A GAM is a special case of a generalized linear model in which smoothing functions are applied to covariates (Hastie and Tibshirani 1990, Wood 2006). We employed GAMs with penalized regression splines, which estimate degree of covariate smoothness with cross validation. An assumption of DCMs is that individuals or groups of individuals make choices to maximize their satisfaction, mirroring assumptions of resource selection functions (Ben-Akiva and Lerman 1985) and have been applied to several wildlife resource selection studies (Cooper and Millspaugh

1999, Baasch et al. 2009; Carter et al. 2010, Unger et al. 2015). We used DCMs because changing habitat availability can be better captured within its framework compared to other recently developed techniques (Cooper and Millspaugh 1999). Additional nest site inclusion throughout the duration of this study was an important consideration, which led to changing habitat availability; as we have data available from 2001 through 2015 on off-channel sites. Results were interpreted using resource functions utilizing a multinomial equation which is denoted as:

$$w(X_{ij}) = \exp(s_1(X_{1ij}) + s_2(X_{2ij}) + \cdots + s_p(X_{pij}))$$

where $X_1 \ldots X_p$ were covariates within choice set (j) if that variable was included in the model (i; Manly et al. 2007). Penalized regression smoothing terms ($s_1 \ldots s_p$) were applied to the covariates to allow for non-linear relationships.

We evaluated our model set using R statistical software (R Core Team 2015) with function gam in package mgcv, which utilizes re-weighting least squares fitting of the penalized likelihood to determine the smoothness of the line and associated degrees of freedom (Wood 2006). Additionally, generalized cross validation was used to determine the penalty for smoothing parameters for each iteration. A smoothing factor of one corresponds to a straight line and the smoothing factor was removed in such cases. Models were compared using Akaike Information Criterion (AIC) to determine top models and important covariate relationships.

After we identified the top model(s), we predicted the probability of resource use for the observed range of values for each covariate in the model and presented relationships graphically. The uncertainty in probability of use was represented by 5$^{th}$ and 95$^{th}$ percentile confidence intervals for each covariate while holding other covariates at their observed mean values. Rug plots were added to each graph to present measures associated with each nest location and available location. Rug plots consisted of a tick mark for each data point where values at probability of use equals one represents nest sites and values equal to zero represent available locations. We also added mirrored histograms to display distributions of nest site locations compared to available locations for variables in the top model(s) to further communicate observed response function relationships. We presented distribution density for each covariate, which sum to one, and allows for a direct comparison of distributions on a common scale to reinforce predicted covariate relationships observed.

To validate the performance of the best model, we partitioned our data randomly into 4 groups of similar size. Training datasets included three of the groups and the fourth group was used to test model performance. We performed chi-squared contingency table analyses with the test datasets for each species, as presented in Howlin et al. 2004. This method was specifically developed to understand the reliability of a binary response (use/available) model. Predicted values of available locations within the test dataset were scaled to the number of use locations in the test dataset. These were then binned into twenty percentile categories and compared to the number of test dataset use locations in each bin. Predicted values were summed to calculate the number of expected use locations in each bin, which were then compared to the actual sum of use locations in each bin with a linear regression to identify the reliability of the model based on the closeness of the slope-relationship of 1. "Good" models had a slope of 1 and a 95% confidence interval that did not incorporate zero. "Adequate" models had a slope >0, but <1 with a 95% confidence interval that did not incorporate zero. If slope-relationships had a 95% confidence interval spanning zero, the model was deemed "Poor."

In addition, a 4-fold cross validation was performed with the training dataset (Howlin et al. 2004). The model was fit with 75% of the original training data and tested for validation with the remaining 25% of the data, for a total of 4 unique iterations. The linear relationship between predicted and actual use locations was also evaluated with "Good," "Adequate," and "Poor" scoring as described above.

## RESULTS

We documented 947 least tern nests and 323 piping plover nests within all managed off-channel sites, 2001–2015. Least tern and piping plover nest and breeding pair counts generally increased after 2009 when the Program began constructing additional off-channel habitat (Fig. 4). The amount of available nesting habitat at all managed sites was fairly consistent from 2001 to 2009, increased from 2010 to 2013 and then remained fairly stable through 2015 (Fig. 2). Nesting density of least terns across all managed off-channel sites was approximately 2.25 breeding pair per hectare and piping plovers averaged about 0.77 breeding pair per hectare (Fig. 3; Tables 3 and 4).

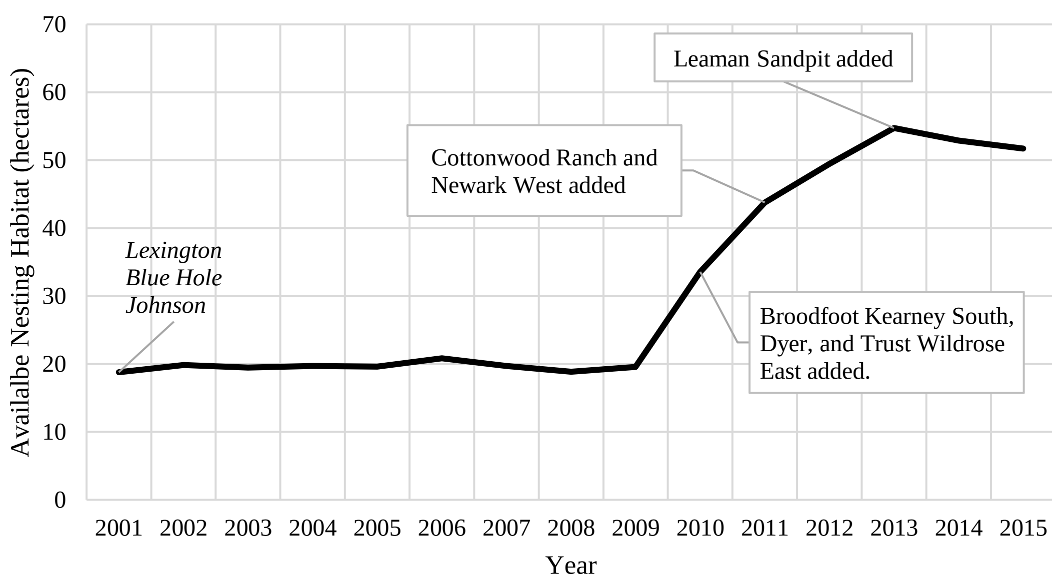



**Figure 2.** Amount of available managed, off-channel nesting habitat within the AHR, 2001–2015. Labels after 2001 indicate when nest sites were first developed and managed for interior least terns (*Sternula antillarum athalassos*) and piping plovers (*Charadrius melodus*). Available nesting habitat decreased slightly from 2013 to 2015 due to increased water surface elevation associated with the extended high-flow events.

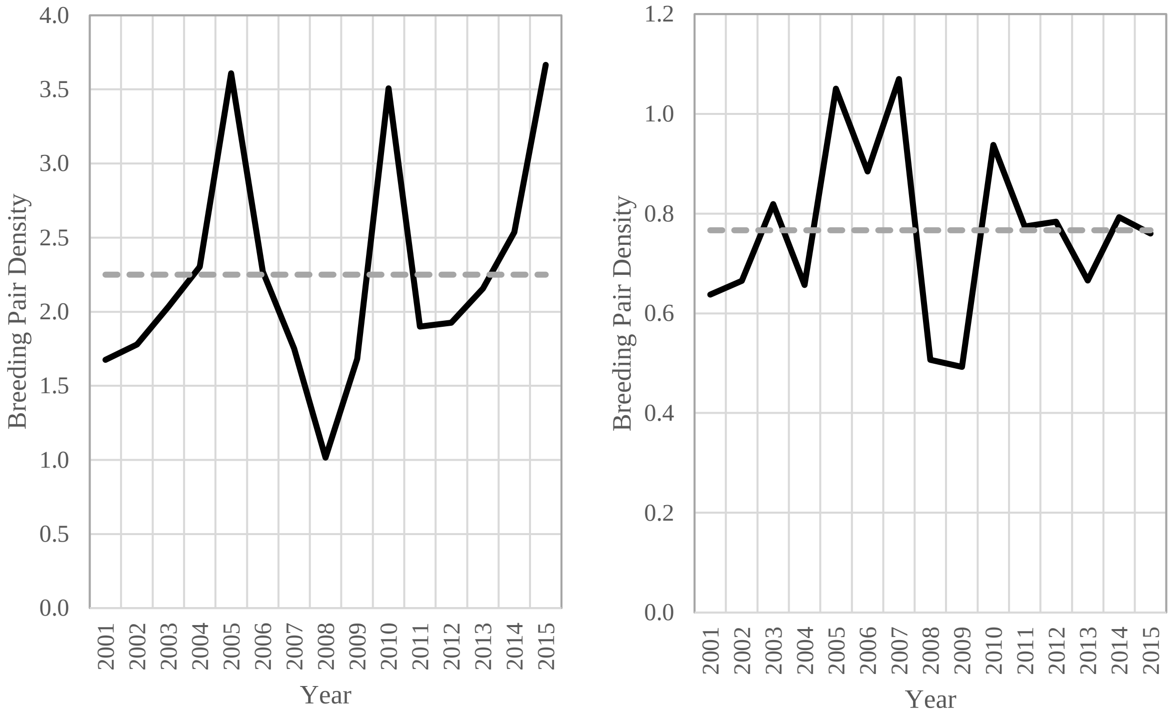


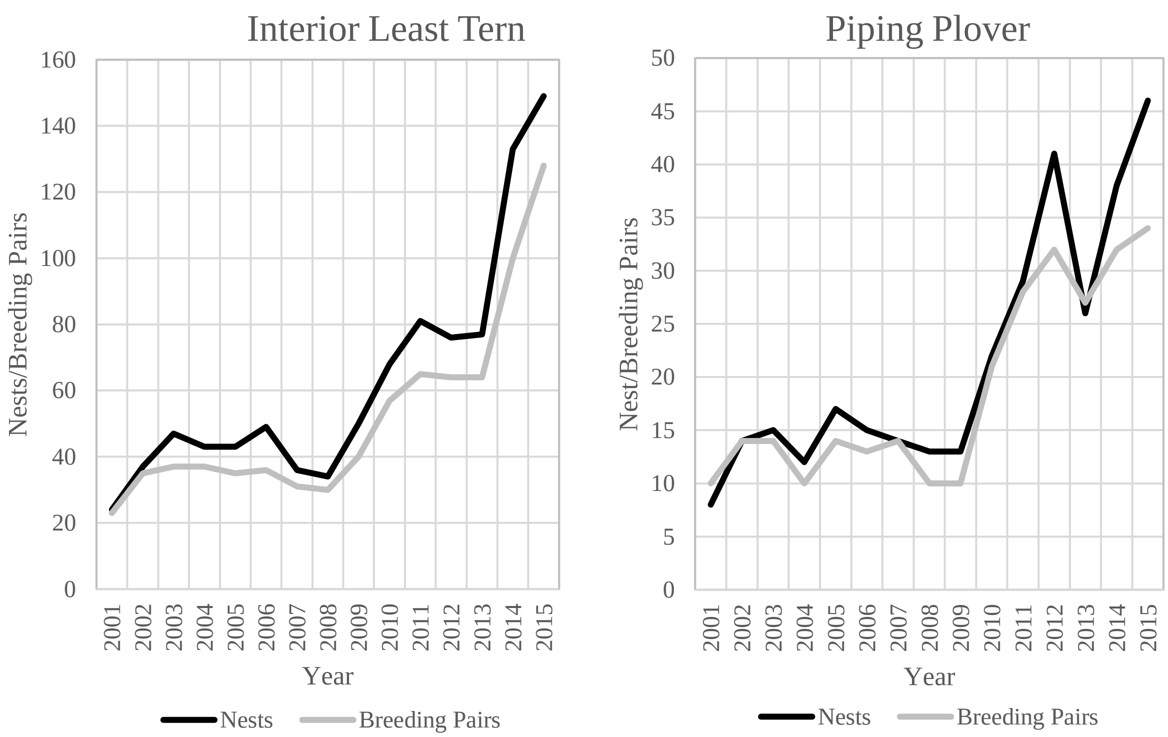

**Figure 3.** Least tern (left) and piping plover (right) annual breeding pair density at managed, off-channel sites within the AHR. Average breeding pair densities are represented as dashed lines.

**Table 3.** Summary of interior least tern (*Sternula antillarum athalassos*) nest and breeding pair counts at managed, off-channel sites.

| Site | Area (ha) | First Nesting Season | Average Nests and SD | Nests per Hectare | Pairs per Hectare |
|---|---|---|---|---|---|
| Lexington Sandpit | 6.6 | Prior to 2001 | 12.5 (7.1) | 1.88 | 1.53 |
| Dyer Sandpit | 8.4 | 2010 | 8.3 (3.6) | 0.99 | 0.58 |
| Cottonwood Ranch Sandpit | 6.8 | 2011 | 8.4 (9.0) | 1.23 | 0.82 |
| Blue Hole | 10.8 | Prior to 2001 | 20.3 (7.3) | 1.89 | 1.57 |
| Johnson Sandpit | 2.0 | Prior to 2001 | 5.7 (4.6) | 2.84 | 2.39 |
| Broadfoot Kearney South | 6.6 | 2010 | 13.3 (6.8) | 2.02 | 1.62 |
| Newark West | 5.5 | 2011 | 14.0 (10.4) | 2.56 | 1.87 |
| Leaman Sandpit | 4.5 | 2013 | 28.7 (19.7) | 6.31 | 4.84 |
| Trust Wildrose East | 1.1 | 2008 | 12 (4.0) | 10.84 | 7.57 |

261 **Table 4.** Summary of piping plover (*Charadrius melodus*) nest and breeding pair counts at
262 managed, off-channel sites.

| Site | Area (ha) | First Nesting Season | Average Nests and SD | Nests per Hectare | Pairs per Hectare |
|---|---|---|---|---|---|
| Lexington Sandpit | 6.6 | Prior to 2001 | 4.5 (1.6) | 0.68 | 0.37 |
| Dyer Sandpit | 8.4 | 2010 | 4.0 (2.3) | 0.48 | 0.61 |
| Cottonwood Ranch Sandpit | 6.8 | 2011 | 0.8 (1.1) | 0.12 | 0.12 |
| Blue Hole | 10.8 | Prior to 2001 | 7.4 (3.4) | 0.69 | 0.68 |
| Johnson Sandpit | 2.0 | Prior to 2001 | 2.2 (1.4) | 1.09 | 0.90 |
| Broadfoot Kearney South | 6.6 | 2010 | 6.8 (3.8) | 1.03 | 0.42 |
| Newark West | 5.5 | 2011 | 2.3 (2.3) | 0.42 | 0.66 |
| Leaman Sandpit | 4.5 | 2013 | 3.3 (2.5) | 0.73 | 0.71 |
| Trust Wildrose East | 1.1 | 2008 | 3.0 (0.6) | 2.71 | 1.92 |




263
264 **Figure 4.** Interior least tern (*Sternula antillarum athalassos*; left) and piping plover (*Charadrius*
265 *melodus*; right) nest counts and breeding pairs by year at managed, off-channel sites within the
266 AHR.

**Table 5**. Average and standard deviation (SD) of covariates included in the *a priori* models for interior least tern (*Sternula antillarum athalassos*) and piping plover (*Charadrius melodus*) nest site selection analyses. Values are presented in meters for all covariates.

| Covariate | Abbreviation | Interior Least Tern | | Piping Plover | |
|---|---|---|---|---|---|
| | | Use | Available | Use | Available |
| Distance to Predator Perch | DPP | 167 (58) | 159 (65) | 167 (63) | 161 (72) |
| Elevation Above Water | EAW | 2 (1) | 2 (1) | 2 (1) | 2 (1) |
| Distance to Edge of Water | DEW | 35 (23) | 25 (18) | 36 (18) | 25 (19) |
| Distance to Least Tern Nest | LTN | 26 (25) | 26 (26) | 15 (36) | 24 (56) |
| Distance to Piping Plover Nest | PPN | 27 (31) | 35 (29) | 131 (101) | 117 (89) |
| Waterline Length | WLL | ----- | ----- | 133 (79) | 148 (66) |

*Nest Site Selection*

Least terns and piping plovers generally selected similar physical site attributes at nest site locations based on the central tendencies and distributions of each covariate (Table 5). Mirrored histograms displaying distribution of covariate values at least tern and piping plover nest site and available locations can be found in Appendices 1 and 2, respectively. Based on the AIC model selection process we found the model containing all covariates except waterline length best explained nest site selection at managed, off-channel sites within the AHR for both species (Table 6).

**Table 6.** Top five nest site selection models as ranked by AIC for interior least terns (*Sternula antillarum athalassos*; left) and piping plovers (*Charadrius melodus*; right). The ΔAIC for the null model for interior least tern and piping plover was 493 and 194, respectively.

| Interior Least Tern | | | Piping Plover | | |
|---|---|---|---|---|---|
| **Model** | **AIC** | **ΔAIC** | **Model** | **AIC** | **ΔAIC** |
| EAW+DPP+PPN+LTN+DEW | 14618 | 0 | EAW+DPP+PPN+LTN+DEW | 4439 | 0 |
| EAW+DPP+DEW | 14632 | 14 | EAW+DPP+DEW | 4478 | 39 |
| DEW | 14773 | 156 | DEW+LTN+PPN | 4490 | 51 |
| EAW+DPP+LTN+PPN | 14797 | 179 | EAW+DPP+PPN+LTN+WLL | 4498 | 59 |
| EAW+DPP+LTN | 14806 | 188 | DEW+DPP | 4504 | 65 |

Our results indicate all covariates tested except waterline length influence nest site selection for least terns and piping plovers. For least terns, positive relationships were indicated for each physical site characteristic and negative relationships were indicated for inter- and intra-specific interactions. Least terns generally chose to nest in locations higher in elevation, farther away from predator perches, and farther away from the water's edge than availability would indicate. Furthermore, least terns nested closer to other least tern and piping plover nests than availability would indicate. Predictive relative probability of least tern use was maximized at 207.1 m to predator perch, 7.3 m above the waterline, 89.0 m to the edge of the nearest water and <1.0 m to the nearest least tern and piping plover nest (Fig. 5). The estimated degrees of freedom for the smoothed terms were 4.11 for DPP, 3.73 for EAW, 5.71 for DEW, 3.86 for LTN, and 4.74 for PPN.

Similarly, piping plovers generally nested at locations higher in elevation, farther away from predator perches, and further away from the water's edge than availability would indicate. Results also indicated that piping plovers nested closer to least tern nests and farther away from other piping plover nests than availability would indicate. Predicted relative probability of use was maximized at 3.2 m above the waterline, 151.0 m to predator perch, 55.3 m to the nearest edge of water, <1 m to the nearest least tern nest, and 346.0 m to the nearest piping plover nest (Fig. 6). The estimated degrees of freedom for the smoothed terms was 5.43 for DPP, 2.97 for EAW, 3.53 for DEW, 1.94 for LTN, and 4.34 for PPN.

We found the best model for both species were adequate to good when evaluating the test dataset and 4-fold cross validation of the training dataset. Evaluating the test dataset (n=80 use locations for piping plovers and n=236 use locations for least terns) resulted in an adequate model fit with linear slope relationships of 0.59 (0.39-0.81; ± 95% CI) for least terns and 0.66 (0.46-0.85; ± 95% CI) for piping plovers (Fig. 7; Table 7). Results of cross validation tests also indicate our least tern and piping plover model performances were adequate to good (Table 8). Visual representations of model results for least terns and piping plovers at a suitable nesting site within the AHR also indicates our model predicted species use fairly well (Figure 8).

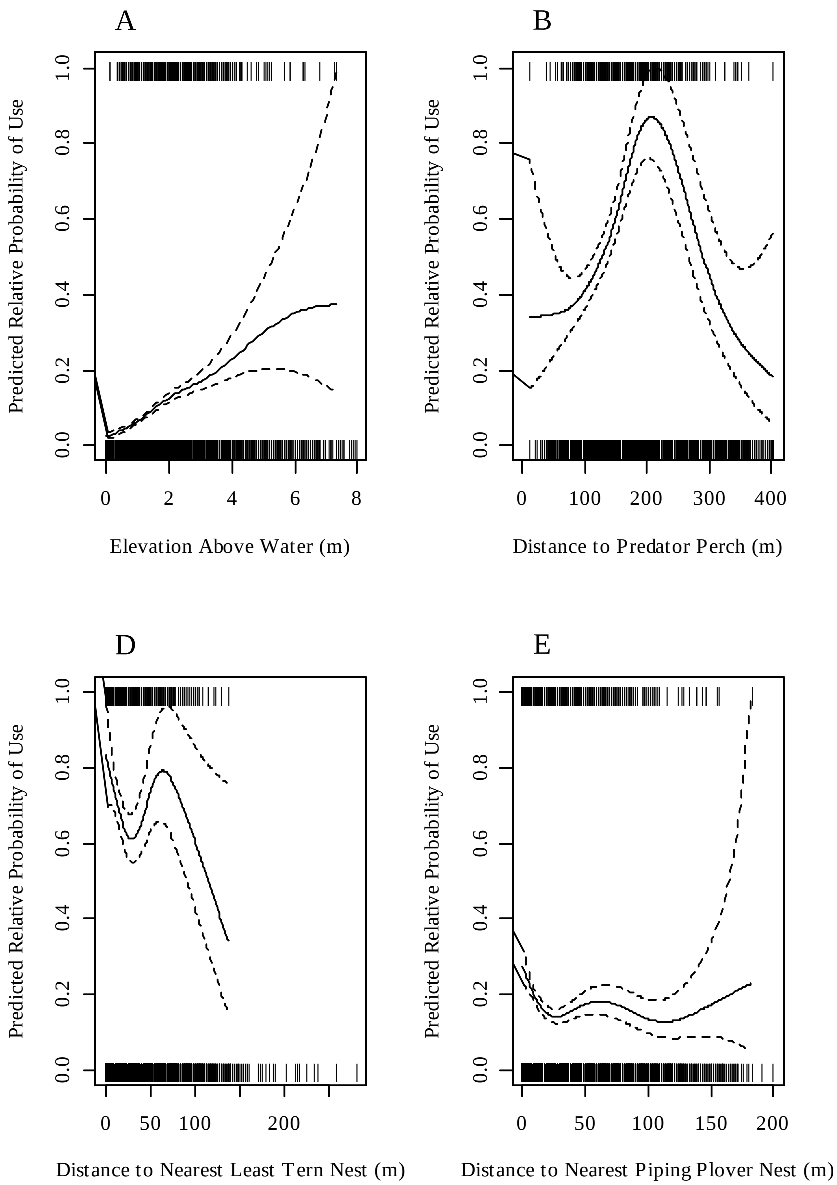



**Figure 5.** Influence of elevation above water (A) and distances to predator perch (B), edge of water (C), nearest interior least tern nest (D), and nearest piping plover nest (E), with 90% confidence intervals, on predicted relative probability of interior least tern (*Sternula antillarum athalassos*) nest site selection. Tick marks at y = 0 and y = 1 indicate the distribution of use and available locations, respectively. Graphs are displayed to various percentiles of nest site locations to minimize the influence of a few extreme values.

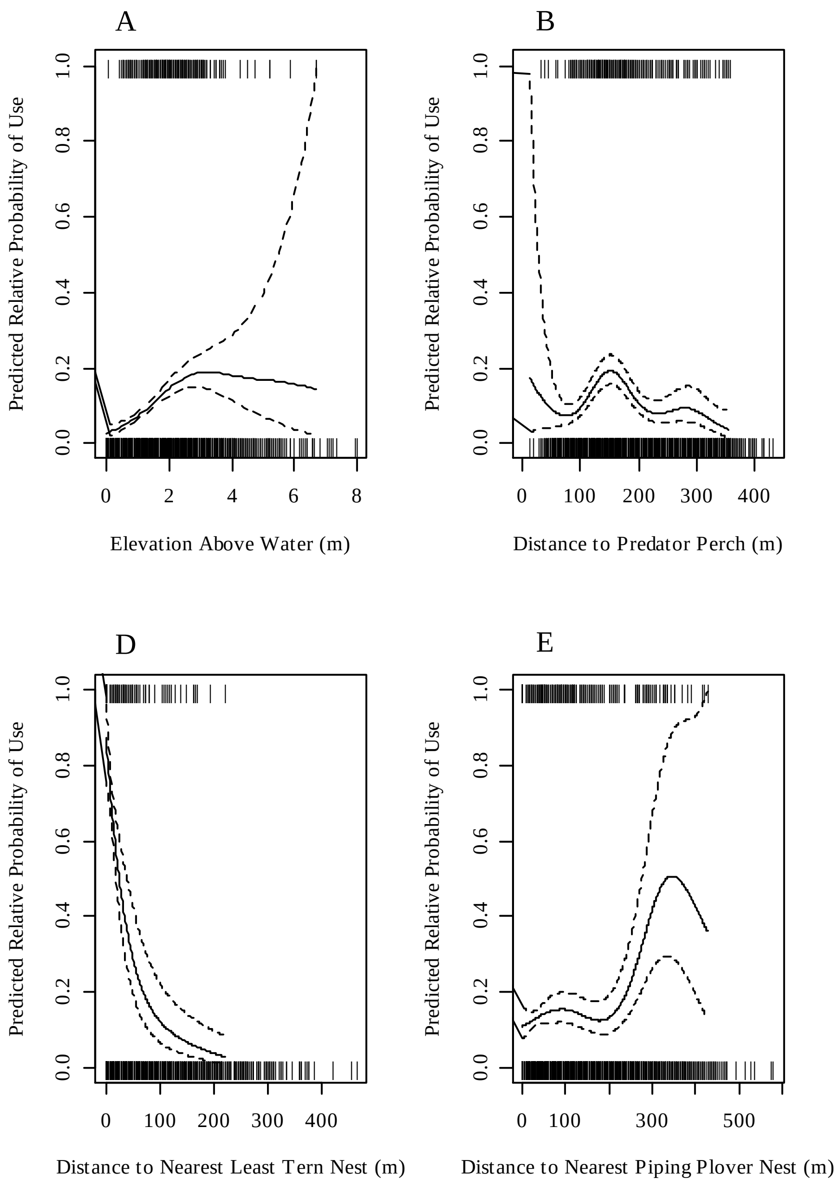



**Figure 6.** Influence of elevation above water (A) and distances to predator perch (B), edge of water (C), nearest interior least tern nest (D), and nearest piping plover nest (E), with 90% confidence intervals, on predicted relative probability of piping plover (*Charadrius melodus*) nest site selection. Tick marks at y = 0 and y = 1 indicate the distribution of use and available locations, respectively.

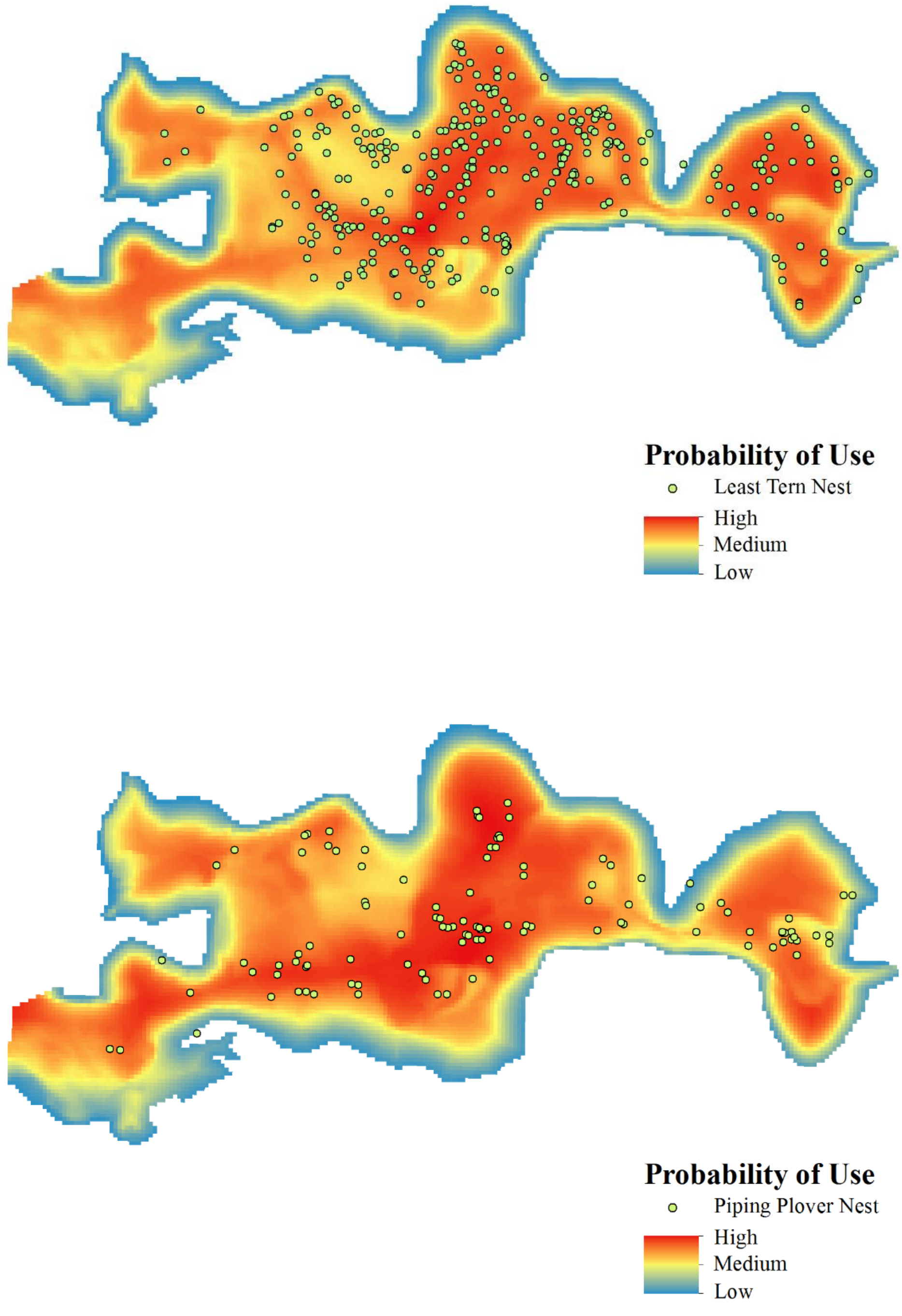



**Figure 7.** Predicted relative probability of use of interior least terns (*Sternula antillarum athalassos*; top) and piping plovers (*Charadrius melodus*; bottom) at an off-channel nesting site (Bluehole) along the central Platte River.

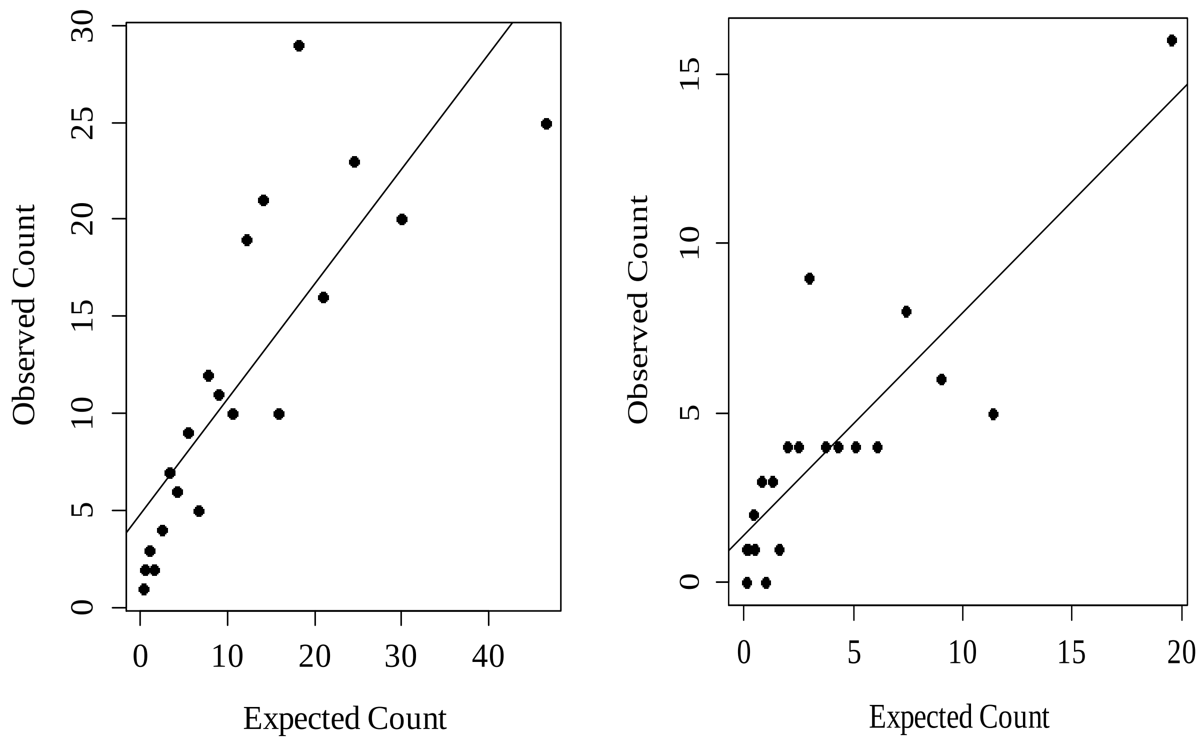



**Figure 8.** Relationship between observed and expected counts in 20 percentile bins to evaluate performance of nest site selection models with the testing dataset for interior least tern (*Sternula antillarum athalassos*; left) and piping plover (*Charadrius melodus*; right). Dashed lines represent predicted linear relationships and points are observed counts within each bin.

**Table 7.** The expected and actual number of use locations in each percentile bin used to evaluate model performance with the testing dataset.

| Least Tern | | | Piping Plover | | |
|---|---|---|---|---|---|
| Bin | Expected Use | Observed Use | Bin | Expected Use | Observed Use |
| 1 | 0.3 | 1 | 1 | 0.1 | 1 |
| 2 | 0.6 | 2 | 2 | 0.1 | 0 |
| 3 | 1.0 | 3 | 3 | 0.2 | 1 |
| 4 | 1.6 | 2 | 4 | 0.4 | 2 |
| 5 | 2.4 | 4 | 5 | 0.5 | 1 |
| 6 | 3.3 | 7 | 6 | 0.8 | 3 |
| 7 | 4.3 | 6 | 7 | 1.0 | 0 |
| 8 | 5.4 | 9 | 8 | 1.3 | 3 |
| 9 | 6.7 | 5 | 9 | 1.6 | 1 |
| 10 | 7.8 | 12 | 10 | 2.0 | 4 |
| 11 | 9.0 | 11 | 11 | 2.5 | 4 |
| 12 | 10.5 | 10 | 12 | 3.0 | 9 |
| 13 | 12.2 | 19 | 13 | 3.7 | 4 |
| 14 | 14.0 | 21 | 14 | 4.3 | 4 |
| 15 | 15.9 | 10 | 15 | 5.1 | 4 |
| 16 | 18.2 | 29 | 16 | 6.1 | 4 |
| 17 | 21.0 | 16 | 17 | 7.4 | 8 |
| 18 | 24.5 | 23 | 18 | 9.0 | 6 |
| 19 | 29.9 | 20 | 19 | 11.4 | 5 |
| 20 | 46.4 | 25 | 20 | 19.5 | 16 |

**Table 8.** Summary of 4-fold cross validation results for the best nest site selection model for interior least tern (*Sternula antillarum athalassos*) and piping plover (*Charadrius melodus*).

| Species | Iteration | # Used Observations | Slope Estimate | Std. Error | p-value | 95% CI on Slope | | Predictive Ability |
|---|---|---|---|---|---|---|---|---|
| | | | | | | Lower | Upper | |
| Least Tern | 1 | 236 | 0.61 | 0.10 | <0.001 | 0.40 | 0.82 | Adequate |
| | 2 | 237 | 0.77 | 0.12 | <0.001 | 0.52 | 1.02 | Good |
| | 3 | 237 | 0.97 | 0.07 | <0.001 | 0.82 | 1.12 | Good |
| | 4 | 237 | 0.89 | 0.06 | <0.001 | 0.76 | 1.02 | Good |
| Piping Plover | 1 | 80 | 0.66 | 0.09 | <0.001 | 0.46 | 0.86 | Adequate |
| | 2 | 81 | 1.01 | 0.12 | <0.001 | 0.76 | 1.27 | Good |
| | 3 | 81 | 0.78 | 0.10 | <0.001 | 0.57 | 1.00 | Adequate |
| | 4 | 81 | 0.75 | 0.09 | <0.001 | 0.57 | 0.93 | Adequate |

## DISCUSSION

We observed an increase in numbers of breeding pairs observed for both species at off-channel sites from 2008–2015; however, breeding pair densities, while variable, did not change. The increase in numbers of birds coincides with increased habitat availability through expansion of existing off-channel sites and acquisition, development, and management of new sites. Based on trends in breeding pair counts and managed, off-channel habitat availability, we believe least terns and piping plovers were habitat limited in the AHR prior to 2009. In 2001, there were approximately 19.4 ha of managed, off-channel habitat in the AHR and only 24 nests and 23 pair of least tern and 8 nests and 10 pair of piping plovers were observed (Baasch et al. 2015, Cahis and Baasch 2016). By 2015 there were approximately 52.3 ha of managed, off-channel nesting habitat and 149 nests and 128 pair of least tern were observed and 46 nests and 34 pair of piping plovers were observed.

We found both inter- and intra-specific competition and attraction and manageable physical site attributes were important predictors of probability of selection for both species at managed off-channel sites. Both species were found to nest closer to already establish least tern nests than availability would indicate. These breeding pairs may have identified important physical attribute resources similarly and selected the best resources available to maximize survival and fitness (Manly et al. 2007). Nesting closer may have increased anti-predator responses and decreased targeting of individual nests by predators (Burger 1988). For the non-gregarious piping plover, individual nest placements near least terns could have added anti-predator benefits compared to solitary nesting behavior (Burger 1987). On the contrary, piping plover nest site selection increased greatly as distance to nearest piping plover nest increased, which is likely due to intra-specific territoriality of piping plovers (Cairns 1982). Observations have confirmed this general territoriality in the AHR, where average piping plover nest densities at managed off channel sites are about 1 nest per 2 ha and obvious intra-specific territorial aggression is regularly observed (Cahis et al. 2016).

When considering physical attributes, least tern and piping plover exhibit similar selection preferences for nesting locations at off-channel sites. Selection and maximum probability of use was similar for EAW, DPP, and DEW for both species. Nest inundation can be major contributor to nest loss depending on nest site characteristics and immediate water resource dynamics. Even though water resource dynamics at off-channel sites are not as extreme as in-channel dynamics, a selection was made to use higher locations with less probability of inundation. Along with inundation, predation can be a major contributor to decreased productivity (Kirsch 1996, Catlin et al. 2011). Nesting least terns and piping plovers generally avoid close predator perches to reduce avian predation potential, which followed the pattern of nesting we observed (Kruse et al. 2001). Distance to edge of water was considered similar to elevation, where sufficient distance was needed to limit nest inundation possibilities. In most cases, manipulation of these important attributes is possible under management plans and nesting trends can be utilized to update habitat requirements.

Habitat management activities implemented at off-channel sites to date have been sufficient for maintaining high levels of productivity for interior least terns and piping plovers along the central Platte River. However, our results suggest additional measures such as removal of woody vegetation ≤150–200 m from off-channel nesting areas would increase the likelihood of additional nesting. Our results also suggest off-channel habitat within the AHR may be at or near the preferred carrying capacity for piping plovers. This would suggest adding additional sites or otherwise increasing the amount of available nesting habitat would result in increased use of off-channel sites. Building upon the current understanding of off-channel site utility for productivity, we now have a greater understanding of how both species use AHR off-channel sites for nesting and how physical site attributes and inter- and intra-specific competition and attraction influence nest site selection. Such information can be used to guide the creation and management of habitat to increase the potential for nesting on off-channel sites.

## LITERATURE CITED

Baasch, D.M., A.J. Tyre, S.E. Hygnstrom, J.J. Millspaugh, K.M. Eskridge, and K.C. VerCauteren. 2009. An evaluation of three statistical methods used in resource selection modeling. *Ecological Modeling* 221:565-574.

Baasch, D.M., T.J. Hefley, and S.D. Cahis. 2015. A comparison of breeding population estimators using nest and brood monitoring data. Ecology and Evolution 4197:4209. doi: 10.1002/ece3.1680. Available at: https://www.platteriverprogram.org/PubsAndData/ProgramLibrary/Baasch et al 2015_Comparison of Breeding Population Estimators.pdf

Ben-Akiva, M.E. and S.R. Lerman. 1985. Discrete choice analysis: theory and application to travel demand (Vol. 9). MIT press.

Burger, J. 1987. Physical and social determinants of nest-site selection in piping plover in New Jersey. *Condor* 89:811–818.

Burger, J. 1988. Social attraction in nesting least terns: effects of numbers, spacing, and other pair bonds. *Condor* 90:575–582.

Cairns, W.E. 1982. Biology and behavior of breeding piping plovers. *The Wilson Bulletin* 94:531–545.

Cahis, S.D. and D.M. Baasch. 2016. Platte River Recovery Implementation Program: 2014 interior least tern and piping plover monitoring and research report for the central Platte River, Nebraska. Prepared for the Platte River Recovery Implementation Program. Available at: https://www.platteriverprogram.org/PubsAndData/ProgramLibrary/PRRIP 2016_Tern and Plover

Carter, N.H., D.G. Brown, D.R. Etter, and L.G. Visser. 2010. American black bear habitat selection in northern Lower Peninsula, Michigan, USA, using discrete-choice modeling. *Ursus* 21:57–71.

Catlin, D. H., J. H. Felio, and J. D. Fraser. 2011. Effect of great-horned owl trapping on chick survival in piping plovers. *Journal of Wildlife Management* 75:458–462.

Cohen J.B., L.M. Houghton, and J.D. Fraser. 2007. Nesting Density and Reproductive Success of Piping Plovers in Response to Storm- and Human-Created Habitat Changes. *Wildlife Monographs* 173:1–24.

Cooper, A.B. and J.J. Millspaugh. 1999. The application of discrete choice models to wildlife resource selection studies. *Ecology* 80:566–575.

Darling, F.F. 1938. Bird flocks and the breeding cycle; a contribution to the study of avian sociality. Oxford, England 134pp.

Elliott-Smith, E. and S.M. Haig. 2004. Piping plover (*Charadrius melodus*). Account 002 in A. Poole, editor. The birds of North America online. Cornell Lab of Ornithology, Ithaca, New York, USA.

Faanes, C.A. 1983. Aspects of the nesting ecology of least terns and piping plovers in central Nebraska. *Prairie Naturalist* 15:145–154.

Fretwell, S. D., and H. L. Lucas. 1970. On territorial behavior and other factors influencing habitat distribution in birds. I. Theoretical development. *Acta Biotheoretica* 19:16–36.

Hastie, T.J. and R.J. Tibshirani. 1990. Generalized additive models (Vol. 43). CRC Press.

Howlin, S., W. P. Erickson, and R. M. Nielson. 2004. A validation technique for assessing predictive abilities of resource selection functions. Pages 40–51 *in*. Proceedings of the first international conference on resource selection Laramie, Wyoming.

Kirsch, E.M. 1996. Habitat selection and productivity of least terns on the lower Platte River, Nebraska. *Wildlife Monographs* 132:3–48.

Kruse, C. D., K. F. Higgins, and B. A. Vander Lee. 2001. Influence of predation on piping plover, *Charadrius melodus*, and least tern, *Sterna antillarum*, productivity along the Missouri River in South Dakota. *Canadian Field-Naturalist* 115:480–486.

Manly, B.F.L., L. McDonald, D. Thomas, T.L. McDonald, and W.P. Erickson. 2007. Resource selection by animals: statistical design and analysis for field studies. Springer Science & Business Media.

Maxson, S.J. 2000. Interspecific interactions of breeding piping plovers: conservation implications. *Waterbirds* 23:270–276.

McFadden, D. 1978. Modeling the choice of residential location. In: Karlquist, A. (Ed.), Spatial Interaction Theory and Planning Models. North Holland Publishing Company, Amsterdam, The Netherlands, pp. 79–96.

Newton, I. 1992. Experiments on the limitation of bird numbers by territorial behavior. *Biological Reviews* 67:397–411.

Program. 2006. Platte River Recovery Implementation Program Adaptive Management Plan. Available at: https://www.platteriverprogram.org/PubsAndData/ProgramLibrary/PRRIP%202006_Attachment%203_AMP.pdf.

Program 2012. PRRIP tern and plover minimum habitat criteria (DRAFT). Available at: https://www.platteriverprogram.org/PubsAndData/ProgramLibrary/PRRIP%202012_LTPP%20Min%20Habitat%20Criteria_Draft.pdf

Rodenhouse, N.L., T.W. Sherry, and R.T. Holmes. 1997. Site-dependent regulation of population size: a new synthesis. *Ecology* 78:2025–2042.

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

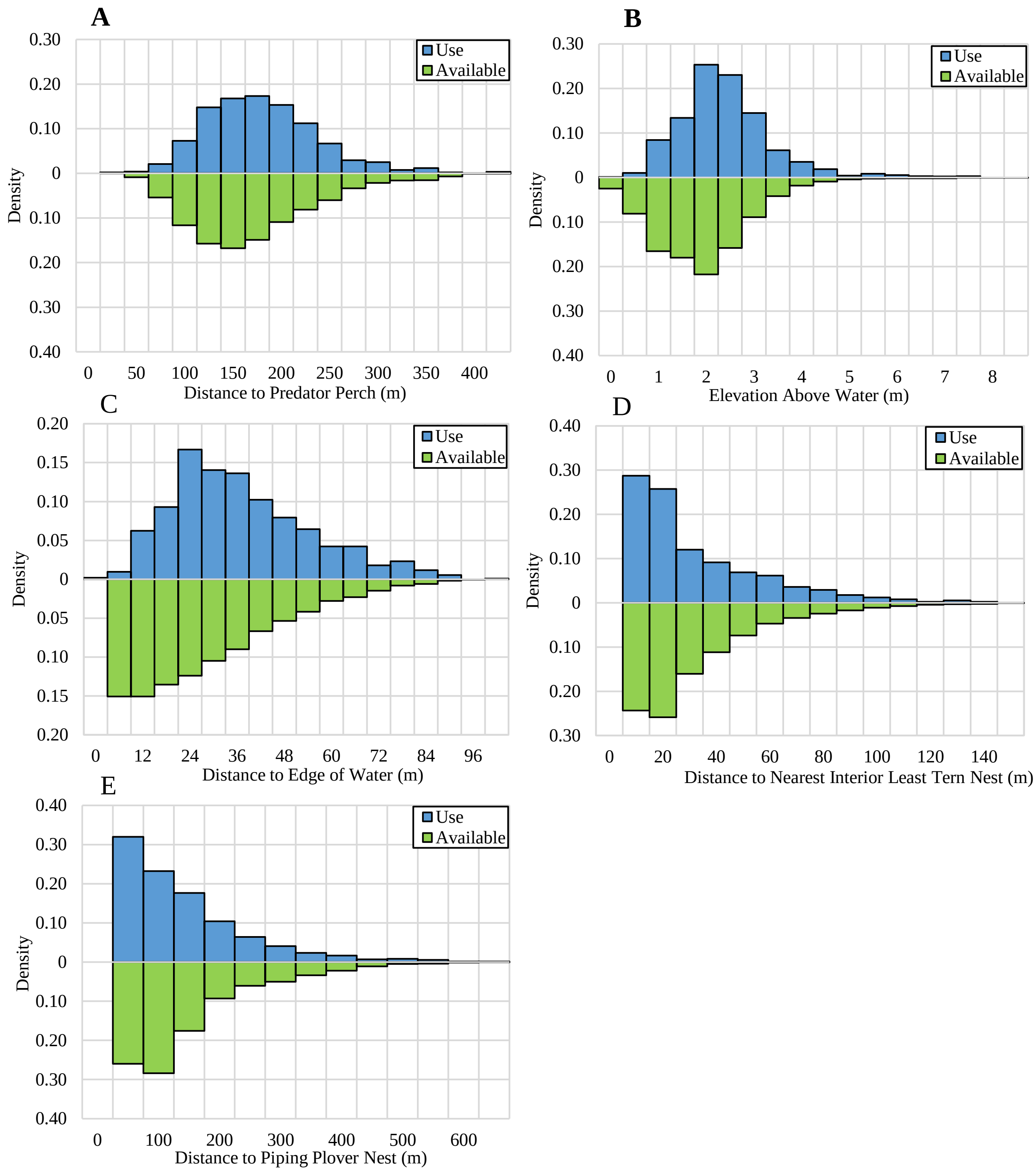
Thompson, B.C., J.J. Jackson, J. Burger, L.A. Hill, E.M. Kirsch, and J.L. Atwood. 1997. Least Tern (*Sterna antillarum*). Academy of Natural Sciences, Philadelphia, PA 32 pp.

Unger, A.M., E.P. Tanner, C.A. Harper, P.D. Keyser, F.T. Van Manen, J.J. Morgan, and D.A. Baxley. 2015. Northern bobwhite seasonal habitat selection on a reclaimed surface coal mine in Kentucky. *Journal of the Southeastern Association of Fish and Wildlife Agencies* 2:235–246.

Wood, S. 2006. Generalized additive models: an introduction with R. CRC Press.

# APPENDICES

**Appendix 1.** Mirrored histograms to compare the distribution densities of physical site and inter- and intra-specific covariate values at interior least tern nest site locations (blue bars) and available locations (green bars). The densities for nest site locations and available locations each sum to one.



**Appendix 2.** Mirrored histograms to compare the distribution densities of physical site and inter- and intra-specific covariate values at piping plover nest site locations (blue bars) and available locations (green bars). The densities for nest site locations and available locations each sum to one.