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Nest-site selection by Interior Least Terns and Piping Plovers at managed, off-channel sites along the Central Platte River in Nebraska, USA

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ABSTRACT. Given the high productivity of Interior Least Terns (*Sternula antillarum athalassos*) and Piping Plovers (*Charadrius melodus*) on constructed off-channel nesting sites along the central Platte River in Nebraska, USA, and the possibility of creating similar habitats at other locations in their breeding range, understanding how these species use off-channel nesting habitats is important. We used data collected along the central Platte River in Nebraska, USA, over a 15-year period (2001–2015), and a discrete-choice modeling framework to assess the effects of physical site attributes and inter- and intraspecific associations on off-channel nest-site selection by Interior Least Terns and Piping Plovers. We found that Piping Plovers avoided nesting near each other, whereas colonial Interior Least Terns selected nest sites near those of conspecifics. In addition, the relative probability of use for both species was maximized when distance to the nearest predator perch was $\geq$ 150 m and elevation above the waterline was $\geq$ 3 m. Probability of use for nesting by Interior Least Terns increased as distance to water increased, whereas the probability of use by Piping Plovers was maximized when distance to water was ~50 m. Our results suggest that important features of constructed, off-channel nesting sites for both species should include no potential predator perches within 150 m of nesting habitat and nesting areas at least 3 m above the waterline. Efficient site designs for Interior Least Terns would be circular, maximizing the area of nesting habitat away from the shoreline, whereas an effective site design for Piping Plovers would be more linear, maximizing the area of nesting habitat near the waterline. An efficient site design for both species would be lobate, incorporating centralized nesting habitat for Interior Least Terns and increased access to foraging areas for nesting and brood-rearing Piping Plovers.

RESUMEN. **Selección de sitio de anidación por *Sternula antillarum* y *Charadrius melodus* en localidades con manejo y fuera del canal a lo largo del tramo central del rio Platte en Nebraska, USA**

Dada la alta productividad de *Sternula antillarum* y *Charadrius melodus* en sitios de anidación construidos fuera del canal a lo largo del tramo central del río Platte en Nebraska, USA y la posibilidad de crear hábitats similares en otras localidades en sus rangos de reproducción, es importante comprender como estas especies usan estos hábitats de anidación fuera del canal. Utilizamos información colectada a lo largo del tramo central del río Platte en Nebraska, USA, a lo largo de un periodo de 15 años (2001–2015) y un marco de modelamiento por selección discreta para determinar el efecto de los atributos físicos y asociaciones inter e intra-específicas en la selección de sitios de anidación fuera del canal por *Sternula antillarum* y *Charadrius melodus*. Encontramos que individuos de *Charadrius melodus* evitan anidar cerca los unos de los otros, mientras que los individuos de *Sternula antillarum,* al ser de anidación colonial, seleccionaron los nidos cerca de con-específicos. Adicionalmente, la probabilidad relativa del uso por las dos especies fue maximizada cuando la distancia a la percha del depredador más cercano fue $\geq$ 150 m y la elevación por encima de la superficie del agua fue $\geq$ 3 m. La probabilidad de uso para anidación por *Sternula antillarum* incrementó con la distancia a la superficie del agua mientras que la probabilidad de uso por *Charadrius melodus* es maximizada cuando la distancia al agua es ~50 m. Nuestros resultados sugieren, que para ambas especies, las características importantes de los sitios de anidación fuera del canal construidos artificialmente no deben incluir perchas para depredadores dentro de 150 m del hábitat de anidación y tener áreas de anidación por lo menos 3 metros por encima de la superficie del agua. Un diseño eficiente para *Sternula antillarum* debe ser circular, maximizando el área del hábitat de anidación lejos de la costa mientras que un diseño efectivo para *Charadrius melodus* debe ser más lineal, maximizando el área del hábitat de anidación cerca de la superficie del agua. Un diseño de los sitios de anidación que sea eficiente para las dos especies, debe ser lobulado, incorporando hábitat de anidación centralizado para *Sternula antillarum* y con mayor acceso a las áreas de forrajeo para anidación y crianza de las nidadas en *Charadrius melodus.*

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Interior Least Terns (*Sternula antillarum athalassos*; hereafter, Least Terns) and Piping Plovers (*Charadrius melodus*) nest in areas with sparse to no vegetation on relatively open bare sand (Patterson 1988, Prindiville-Gaines and Ryan 1988, Sherfy et al. 2008, Catlin et al. 2015). This habitat is found throughout the ranges of both species on in-channel sandbars as well as off-channel and shoreline areas. Several in-channel habitat selection investigations have reported nesting and foraging habitat dynamics, physical site attributes, management strategies, and intraspecific associations that influence nest-site selection by Least Terns and Piping Plovers (Kotliar and Burger 1986, Spear et al. 2007, Maslo et al. 2011, Sherfy et al. 2012b, Catlin et al. 2015).

Proximity to foraging habitat at nesting locations can be especially important for Piping Plovers (Patterson et al. 1991, Loegering and Fraser 1995, Elliott-Smith and Haig 2004, Cohen et al. 2009, Maslo et al. 2011, 2012). Nest sites of Piping Plovers are often near productive foraging areas where they defend territories around nesting and foraging locations, preventing other Piping Plovers and possibly Least Terns from nesting nearby (Cairns 1982, Burger 1987, Patterson et al. 1991, Cohen et al. 2009). Territorial behavior can influence nest-site selection and densities of nests when availability of suitable habitat is limited (Faanes 1983). Cohen et al. (2009) found that rates of population growth were negatively related to density in Piping Plovers. Least Terns, however, are a colonial species (Darling 1938, Burger 1988), so the locations of nest sites may depend on the distribution of the first few nests established at a site (Archibeque 1987, Hillman et al. 2013).

Many investigators have examined the characteristics of nest sites and effects of intraspecific associations on nest-site selection by several species of birds including Least Terns and Piping Plovers (Kolbe and Janzen 2002, Spear et al. 2007, Sherfy et al. 2012b, Catlin et al. 2015). However, no one to date has examined nest-site selection by Least Terns and Piping Plovers on off-channel areas such as sandpits and constructed off-channel nesting areas or included both physical and behavioral attributes in the same models. Further, although the results of some studies suggest that behavioral interactions may influence nest-site selection and that nest-site selection on these off-channel sites may differ from that on in-channel sites (Burger 1988, U. S. Army Corps of Engineers 2011, Sherfy et al. 2012a,b, Lott et al. 2013a,b), these assumptions have not been tested. Nest-site selection on in-channel and shoreline nesting areas may differ from that in off-channel areas due to the relative stability and perceived security of off-channel habitat. Off-channel sites along the central Platte River have permanent water barriers surrounding them, whereas islands sometimes become connected to shorelines when river flows decrease, increasing the likelihood of predation by terrestrial predators. Given the high productivity of Least Terns and Piping Plovers nesting on restored or constructed off-channel nesting sites along the central Platte River in Nebraska (Keldsen and Baasch 2016) and the recent interest in creating similar habitats in other areas in their breeding range (J. Shadle, pers. comm.), understanding how these two species use off-channel nesting habitats is important. Our objective, therefore, was to determine how physical site attributes and density-dependent, inter- and intraspecific associations influenced nest-site selection by Least Terns and Piping Plovers on managed, off-channel sites along the Central Platte River in Nebraska.

METHODS

Study area. The Associated Habitat Reach for the Program is a 145-km reach extending from Lexington, Nebraska, downstream to Chapman, Nebraska, USA, and encompasses central Platte River channels and off-channel habitats (sandpits and constructed off-channel sand and water sites) within 5.6 km of the river. Only three managed, off-channel nesting sites were present in 2001, but creation of new and restoration of existing sites increased the number of nesting sites to nine by 2013 and all were maintained through 2015 (Table 1). Management

Table 1. Off-channel nesting sites along the central Platte River in Nebraska, USA, managed for Interior Least Terns and Piping Plovers. Information presented includes the location (World Geodetic System 1984), the year each site was first managed, and the area of each site.

Site	Latitude	Longitude	Year first managed	Area (ha)
Lexington	40.734815	−99.724912	Prior to 2001	6.6
Dyer	40.677063	−99.553710	2010	8.4
Cottonwood Ranch	40.687807	−99.488689	2011	6.8
Blue Hole	40.686543	−99.369788	Prior to 2001	10.8
Johnson	40.669794	−99.367892	Prior to 2001	2.0
Broadfoot Kearney South	40.664896	−99.098488	2010	6.6
Newark West	40.680855	−98.948538	2011	5.5
Leaman	40.758516	−98.584645	2013	4.5
Trust Wildrose East	40.780913	−98.475562	2008	1.1

activities at each site 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's minimum habitat criteria (Platte River Recovery Implementation Program 2012) to determine the amount of nesting habitat available each year, and a breeding-pair estimator to estimate numbers and densities of breeding pairs (Baasch et al. 2015, Keldsen and Baasch 2016).

Nest location data. During the nesting seasons of 2001 through 2015, all nine nesting sites were 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 the last fledglings or cessation of nesting or brood-rearing activities. Monitoring objectives were to locate and document Least Tern and Piping Plover adults, nests, chicks, fledglings, and breeding pairs. Surveys included observations from > 50 m outside of the nesting habitat area using spotting scopes and binoculars (2001–2015) as well as entering active sites to walk through nesting areas and identify nest locations based on systematic, 10-m grid searches that were conducted at least twice per week (2009–2015; Platte River Recovery Implementation Program 2015a). Active nests were defined as any scrape containing ≥ 1 egg. Active nests were monitored ≥ 2 times per week until successful (≥ 1 chick observed hatched), failed (evidence of nest destruction or abandonment), or unknown fates (no evidence present) were determined. Due to intense survey efforts, we assumed the probability of nest detection was one.

We used Trimble GPS units with sub-meter accuracies to record the location of nests, estimated the nest-initiation date ($\pm$ 0–5 days) by floating eggs (Hays and LeCroy 1971), and collected nest-site data during the initial visit to each nest. Habitat measurements collected off site using ArcMap (ESRI 2011) included elevation above water and distances to nearest waterline and predator perch.

Used and available location data. To populate nest-site-selection models, we collected nest-site data at each managed, off-channel location where a nest was found (nest-site location) as well as at random locations within each site (available locations). We assumed available locations were limited to off-channel sites where nests were found because our study was focused on small-scale (within site) as opposed to macro-scale (between site) habitat selection. Twenty random points were generated in the off-channel site where each nest was located using the Create Random Points tool in ArcMap (ESRI 2011). The 20 random points represented a sample of available locations with associated resources and, with the nest-site location, made up a "choice set" for each individual nesting event (Cooper and Millspaugh 1999). Choice sets of ≤ 20 random points have been found to be sufficient in other studies (McFadden 1978, Baasch et al. 2009, Unger et al. 2015). Each choice set was unique and linked by a likelihood function to the nest-site location using the strata feature in

Program R's gam function (R Development Core Team 2015).

Nest-site characteristics. To reduce error and maintain consistency, aerial photographs (≤ 1-m resolution) taken during the nesting season by the USDA Farm Service Agency National Agriculture Imagery Program (NAIP imagery; 2001–2006) or the Platte River Recovery Implementation Program (2007–2015), and GPS locations of nests were used to determine the distances to the edge of water and the nearest possible predator perch. All distance measures were collected in ArcGIS (ESRI 2011). The distance to the edge of water was defined as the closest Euclidean distance to water from each nest and random location. Because Piping Plovers forage along the edge of the water, we also quantified waterline length within 65 m (based on average nesting density; Keldsen and Baasch 2016) of each Piping Plover nest. Distance to predator perches was defined as the Euclidean distance to the closest wooded area or object ≥ 3 m tall that could be used by an avian or mammalian predator. LiDAR imagery was used to develop digital elevation models to measure elevation above water of the sites. Digital elevation models were used 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 in nesting areas.

Inter- and intraspecific associations. Distances to the nearest Piping Plover nest (PPN) and Least Tern nest (LTN) were calculated based on GPS locations of each nest. We used ArcGIS (ESRI 2011) to identify the Least Tern and Piping Plover nests that were closest to each new Least Tern or Piping Plover nest. Only active nests (i.e., nests that had not failed or succeeded) were considered when determining the closest nests. Due to the inability of our resource selection function to handle missing data points (i.e., no Least Tern or Piping Plover nest present at the nesting site when a nest was established), the newly established nest and associated random locations were assigned a distance measure of 0 m. Nests of Piping Plovers ($N = 278$) and Least Terns ($N = 50$) that were established when no other Least Tern nest was present and nests of Piping Plovers ($N = 78$) and Least Terns ($N = 215$) established when no other Piping Plover nest was present were removed from the summary statistics.

Table 2. A priori models evaluated using discrete-choice models with penalized regression splines for nest-site selection by Interior Least Terns and Piping Plovers. Covariates in our models included elevation above water (EAW), waterline length (WLL), and distances to edge of water (DEW), nearest predator perch or wooded area (DPP), nearest Piping Plover nest (PPN), and nearest Interior Least Tern nest (LTN).

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 developed a priori candidate models, including a null model, to understand how different covariates and combinations of covariates influenced nest-site selection by each species (Table 2). The 36 candidate models consisted of combinations of variables deemed most plausible based on species behavior. We used general additive models (GAMs) within a discrete-choice model framework to develop our models. 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 discrete-choice models 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 these models have been applied to several wildlife resource selection studies (Cooper and Millspaugh 1999, Baasch et al. 2009, Unger et al. 2015). We used discrete-choice models because habitat conditions and availability changed and can be better captured within this framework (Cooper and Millspaugh 1999). 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 (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 Development Core Team 2015) with function gam in package mgcv that uses 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. Smoothing factors > 1 indicate how many curves the line will have in it. Models were compared using Akaike Information Criterion (AIC) to determine the top models and important covariate relationships.

Our training datasets (dataset used to develop the model) included 75% of the data and the remaining 25% of the data were used to test model performance (test dataset). After we identified the top model(s) based on the training data, we predicted the probability of resource use for the observed range of values for each covariate in the model and presented relationships graphically. Uncertainty in probability of use was represented by 5th and 95th percentile confidence intervals for each covariate while holding other covariates at their observed mean values (Long and Freese 2006, Leeper 2017). 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 plotted at one represent nest sites and values plotted at zero represent available locations.

To validate performance of the best model, we partitioned our data randomly into four groups of similar size. We performed chi-squared contingency table analyses with the test datasets for each species (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 20 evenly distributed 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 using linear regression to identify the reliability of the model based on the closeness of the relationship of the slope to one. "Good" models had a slope where the 95% confidence interval included one, but did not include zero. "Adequate" models had a slope > 0 and < 1 with a 95% confidence interval that did not include zero. If relationships of the slope had a 95% confidence interval spanning zero, the model was deemed "Poor" (Howlin et al. 2004).

RESULTS

We located 947 Least Tern nests and 323 Piping Plover nests at the nine nesting sites from 2001 to 2015. The amount of available nesting habitat at all managed sites was relatively constant from 2001 to 2009, increased > 2.5-fold from 2010 to 2013, and then remained relatively stable through 2015 (Fig. 1). Counts of breeding pairs of Least Terns and Piping Plovers increased in proportion to availability of nesting habitat when additional off-channel nesting habitat was

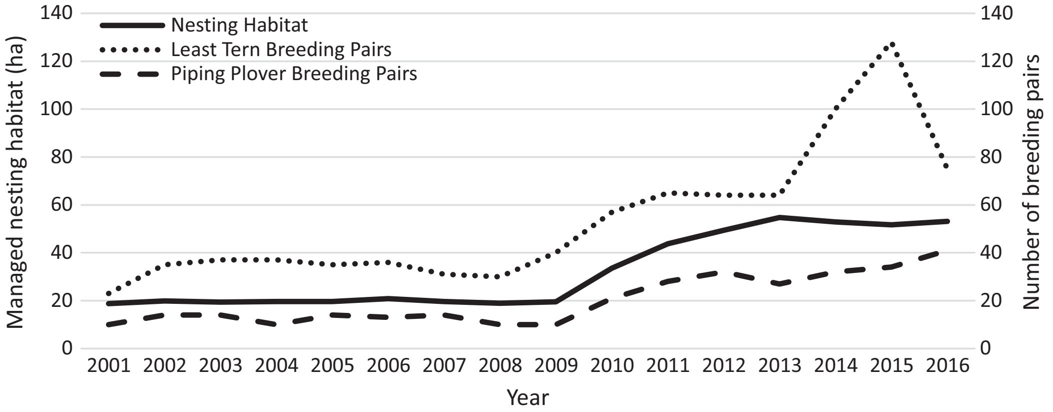

Fig. 1. Amount of managed, off-channel nesting habitat available (solid line) relative to the number of breeding pairs of Interior Least Terns and Piping Plovers along the central Platte River in Nebraska, USA, 2001–2015.

created in 2009 (Fig. 1). Mean nest densities across all managed, off-channel sites were ~2.25 breeding pairs/ha of bare-sand nesting area for Least Terns, and ~0.77 breeding pairs/ha for Piping Plovers (Fig. 2, Table 3) and these densities remained relatively stable throughout our 15-year study (Fig. 2).

Nest-site selection. Nest sites of Least Terns and Piping Plovers had similar characteristics based on the central tendencies and distributions of each covariate (Table 4). Based on the AIC-model-selection process, our results suggest that all covariates tested, except waterline length, influenced nest-site selection by Least Terns and Piping Plovers (Table 5). Nests of Least Terns were generally higher in elevation and farther from predator perches and the water's edge than availability would indicate. Least Terns also nested closer to other nests of Least Terns and Piping Plovers than availability would indicate. While holding the remaining covariates at their mean, predictive relative probability of use by Least Terns was maximized at 207 m from a predator perch, 7.3 m above the waterline, 89 m from the nearest waterline, and < 1.0 m from the nearest Least Tern and Piping Plover nest (Fig. 3). The estimated degrees of freedom for the smoothed terms were 4.11 for distance to nearest predator perch or wooded area, 3.73 for elevation above water, 5.71 for

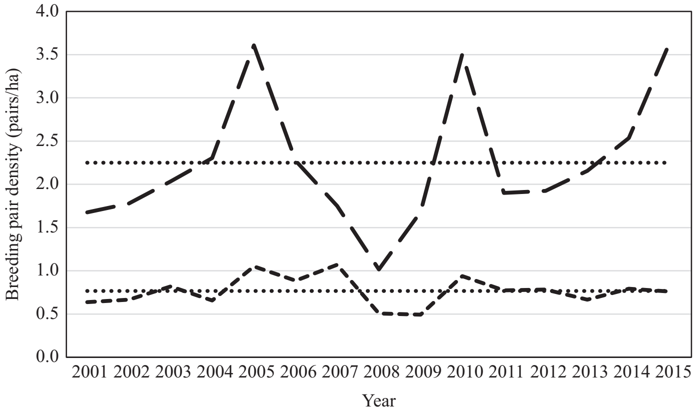

Fig. 2. Annual breeding-pair densities of Interior Least Terns (long dashed line) and Piping Plovers (short dashed line) at nine managed, off-channel sites along the central Platte River in Nebraska. Average breeding-pair densities are represented as dotted lines.

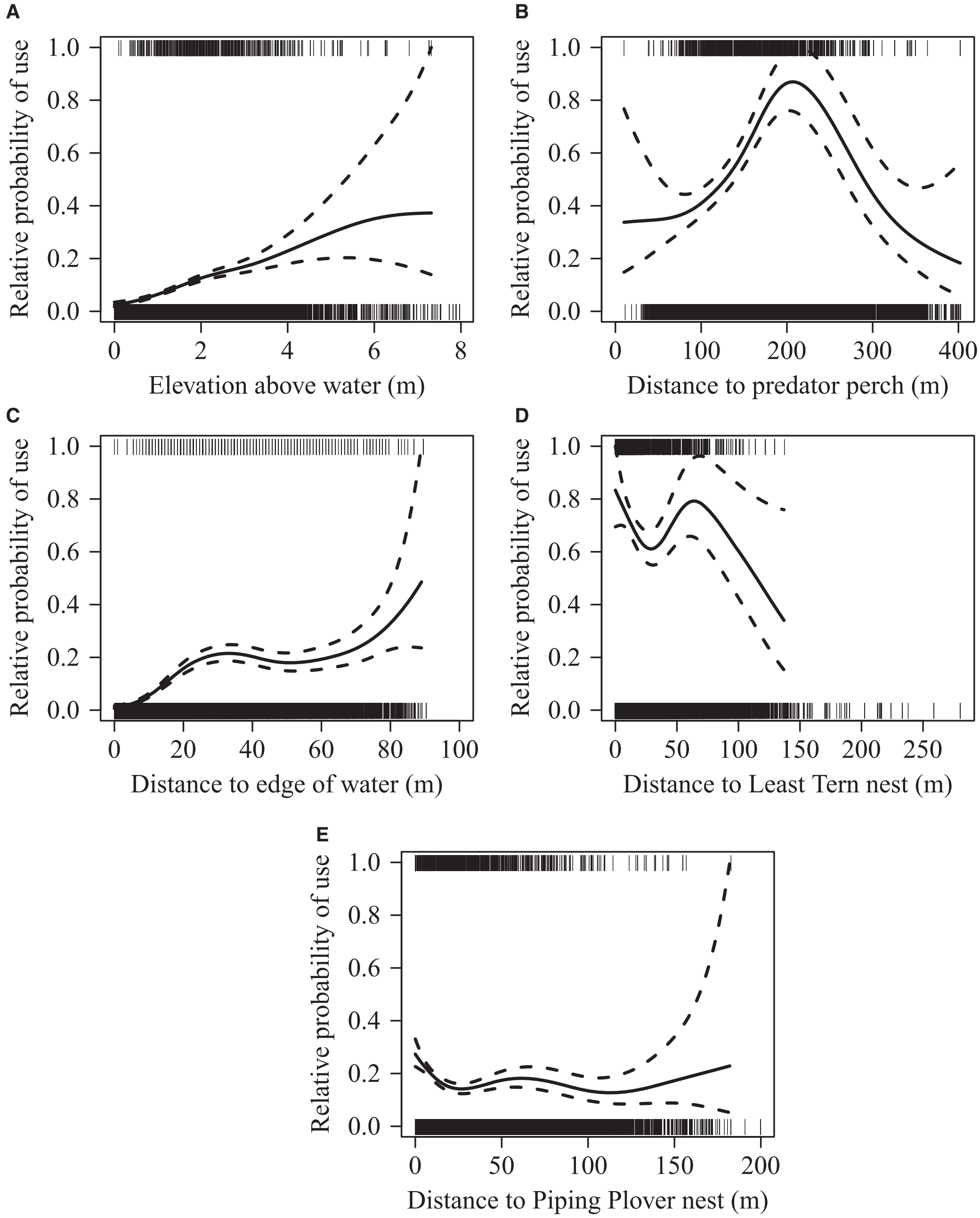

Fig. 3. Influence of (A) elevation above water, and distance to the (B) nearest predator perch, (C) edge of water, (D) nearest Interior Least Tern nest, and (E) nearest Piping Plover nest, with 90% confidence intervals, on the predicted relative probability of nest-site selection by Interior Least Terns. Relative probabilities of use were quantified using discrete-choice models and penalized regression splines while holding the other variables in the model at their mean. Tick marks at $y = 1$ and $y = 0$ indicate the distribution of used and available locations, respectively.

distance to the edge of water, 3.86 for the nearest Least Tern nest, and 4.74 for the nearest Piping Plover nest.

Similarly, Piping Plovers generally nested at locations higher in elevation and farther from predator perches and the water's edge than

Table 3. Numbers and densities of nests and breeding pairs of Interior Least Terns and Piping Plovers at managed, off-channel sites along the central Platte River in Nebraska, USA, over a 15-year period (2001–2015).

			Interior Least Tern			Piping Plover		
Site	Area (ha)	First nesting season	Mean number of nests (SD)	Nests per hectare	Pairs per hectare	Mean number of nests (SD)	Nests per hectare	Pairs per hectare
Lexington	6.6	Prior to 2001	12.5 (7.1)	1.88	1.53	4.5 (1.6)	0.68	0.37
Dyer	8.4	2010	8.3 (3.6)	0.99	0.58	4.0 (2.3)	0.48	0.61
Cottonwood Ranch	6.8	2011	8.4 (9.0)	1.23	0.82	0.8 (1.1)	0.12	0.12
Blue Hole	10.8	Prior to 2001	20.3 (7.3)	1.89	1.57	7.4 (3.4)	0.69	0.68
Johnson	2.0	Prior to 2001	5.7 (4.6)	2.84	2.39	2.2 (1.4)	1.09	0.90
Broadfoot Kearney South	6.6	2010	13.3 (6.8)	2.02	1.62	6.8 (3.8)	1.03	0.42
Newark West	5.5	2011	14.0 (10.4)	2.56	1.87	2.3 (2.3)	0.42	0.66
Leaman	4.5	2013	28.7 (19.7)	6.31	4.84	3.3 (2.5)	0.73	0.71
Trust Wildrose East	1.1	2008	12.0 (4.0)	10.84	7.57	3.0 (0.6)	2.71	1.92

availability would indicate. Piping Plovers also nested closer to Least Tern nests and farther from other Piping Plover nests than availability would indicate. While holding the remaining covariates at their mean, 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. 4). The estimated degrees of freedom for the smoothed terms was 5.43 for distance to nearest predator perch or wooded area, 2.97 for elevation above water, 3.53 for distance to the edge of water, 1.94 for the nearest Least Tern nest, and 4.34 for the nearest Piping Plover nest.

The best models for both species were adequate to good when evaluating the test dataset and four-fold cross-validation of the training dataset. Evaluating the test dataset ($N = 80$ used locations for Piping Plovers and $N = 236$ used locations for Least Terns) resulted in an adequate model fit with linear-slope relationships of 0.61 (0.40–0.82; ± 95% CI) for Least Terns and 0.68 (0.50–0.86; ± 95% CI) for Piping Plovers (Fig. 5). Results of cross-validation tests also indicate that performance of our Least Tern and Piping Plover models was adequate to good (Table 6).

DISCUSSION

Both inter- and intraspecific associations and site characteristics were important predictors of the probability of nest-site selection for both species in our study. When Least Tern nests were present, both species nested closer to active Least Tern nests than availability would indicate. For Piping Plovers, nesting near Least Terns could provide antipredator benefits (Burger 1987, 1988), but they may also have simply selected the best nest site available in an attempt to maximize their survival and fitness (Manly et al. 2007). In contrast, Piping Plovers tended to nest farther from the nests of other Piping Plovers than availability would indicate, likely due to intraspecific territoriality (Cairns 1982).

Maximum relative probability of use was similar for distance to the nearest predator perch for both Least Terns and Piping Plovers, but differed slightly for elevation above

Table 4. Mean values (SD) of covariates included in our discrete-choice models for analyses of nest-site selection by Interior Least Terns and Piping Plovers. Values are presented in meters for all covariates.

Covariate	Interior Least Tern		Piping Plover	
	Used	Available	Used	Available
Distance to predator perch	167 (58)	159 (65)	167 (63)	161 (72)
Elevation above water	2 (1)	2 (1)	2 (1)	2 (1)
Distance to edge of water	35 (23)	25 (18)	36 (18)	25 (19)
Distance to closest Least Tern nest	26 (25)	26 (26)	15 (36)	24 (56)
Distance to closest Piping Plover nest	27 (31)	35 (29)	131 (101)	117 (89)
Waterline length	–	–	133 (79)	148 (66)

Table 5. Top five nest-site-selection, discrete-choice models as ranked by AIC for Interior Least Terns and Piping Plovers. Covariates included elevation above water (EAW), waterline length (WLL), and distances to edge of water (DEW), nearest predator perch or wooded area (DPP), nearest Piping Plover nest (PPN), and nearest Interior Least Tern nest (LTN). The ΔAICs for the null models for Interior Least Terns and Piping Plovers were 493 and 194, respectively.

Interior Least Tern			Piping Plover		
Model	AIC	ΔAIC	Model	AIC	ΔAIC
EAW+DPP+PPN+LTN+DEW	14 618	0	EAW+DPP+PPN+LTN+DEW	4439	0
EAW+DPP+DEW	14 632	14	EAW+DPP+DEW	4478	39
DEW	14 773	156	DEW+LTN+PPN	4490	51
EAW+DPP+LTN+PPN	14 797	179	EAW+DPP+PPN+LTN+WLL	4498	59
EAW+DPP+LTN	14 806	188	DEW+DPP	4504	65

water and distance to edge of water. Although off-channel nesting areas are not subject to many of the high-water events observed with in-channel sandbar sites, nest inundation can be an important cause of nest failure depending on nest-site characteristics (Faanes 1983, Sidle et al. 1992). Nest sites of both species were at higher elevations where the probability of inundation was lower. Probability of nesting for Piping Plovers increased until elevations were about 3 m and then stabilized, whereas Least Terns selected the highest elevations for nesting. Elevations on central Platte River off-channel sites are generally sloped for the first 30–50 m from the waterline and then flatten out at an elevation of 2–4 m, with areas of higher elevation distributed throughout the sites. Lower areas near the waterline provide foraging habitat for Piping Plovers, whereas higher elevations provide additional security from inundation for Least Terns. Faanes (1983) reported that nest elevations of Least Terns and Piping Plovers differed markedly on river islands, suggesting that Least Terns preferred higher and drier nesting habitat than Piping Plovers. Faanes (1983) also reported that the mean height above water of 10 Least Tern nests on one sandbar in the Middle Loup River was 68 cm. Piping Plovers, however, have been found to nest at elevations closer to the water level on the lower Platte River (Ducey 1981).

Proximity to foraging habitat can potentially influence nest-site selection and productivity (Atwood and Kelly 1984, Le Fer et al. 2008, Catlin et al. 2011b, Stucker et al. 2012). Least Terns are known to forage < 100 m from their nesting colonies (Faanes 1983, Schweitzer and Leslie 1996), but have also been reported to use foraging areas > 10 km from their nests (Sherfy et al. 2012a). As such, Least Terns do not need to nest as close to foraging areas and the relative probability of nest-site selection for Least Terns increased with distance to the waterline. In contrast, young Piping Plovers are constrained to foraging in their natal nesting areas and we found that their mean, predicted relative probability of use as a nest site was maximized at 55.3 m from water. Similarly, other investigators have reported that

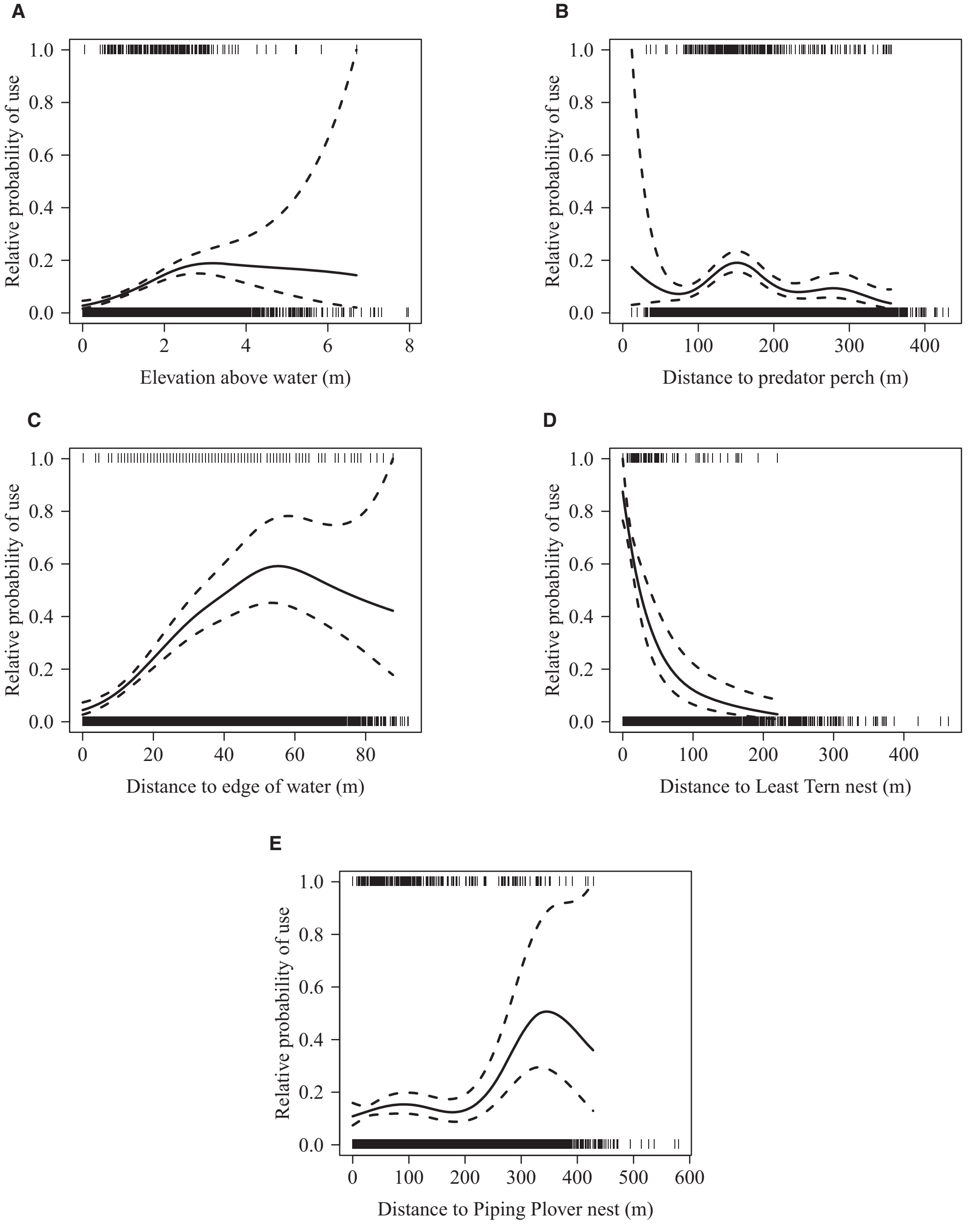

Fig. 4. Influence of (A) elevation above water, and distance to the (B) nearest predator perch, (C) edge of water, (D) nearest Interior Least Tern nest, and (E) nearest Piping Plover nest, with 90% confidence intervals, on the predicted relative probability of nest-site selection by Piping Plovers. Relative probabilities of use were quantified using discrete-choice models and penalized regression splines while holding the other variables in the model at their mean. Tick marks at $y = 1$ and $y = 0$ indicate the distribution of used and available locations, respectively.

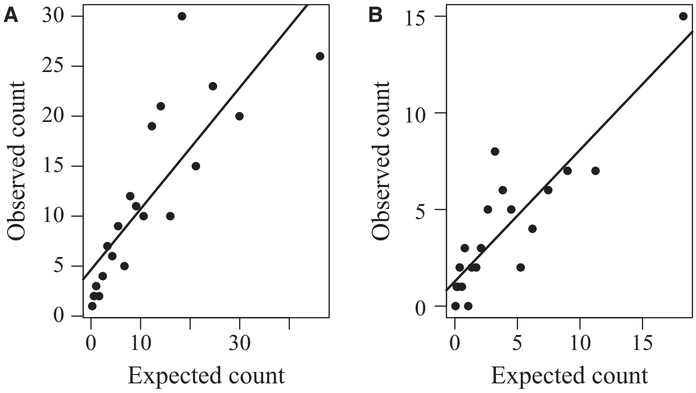

Fig. 5. Relationship between observed and expected counts in 20 percentile bins to evaluate the performance of our discrete-choice, nest-site-selection models with the testing dataset for (A) Interior Least Terns and (B) Piping Plovers. Solid lines represent predicted linear relationships and points are observed counts within each bin.

Table 6. Summary of four-fold cross-validation results for the best discrete-choice, nest-site-selection model for Interior Least Terns and Piping Plovers. Confidence intervals that included one were deemed to have "Good" predictive ability, confidence intervals that contained zero were deemed to have "Poor" predictive ability, and those that did not include one or zero were deemed to have "Adequate" predictive ability (Howlin et al. 2004).

Species	Iteration	No. of used observations	Slope estimate	SE	*P*	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	Good
	4	81	0.75	0.09	< 0.001	0.57	0.93	Adequate

Piping Plovers were less likely to nest farther than ~50 m from the nearest waterline (Patterson et al. 1991, Loegering and Fraser 1995, Cohen et al. 2009).

Predation can also be a major contributor to decreased productivity (Kirsch 1996). Most nest and chick losses for both species at several locations, including off-channel sites in the lower Platte River, off-channel sites in New Jersey, and at Assateague Island, have been attributed to predation (Kotliar and Burger 1986, Patterson et al. 1991, Kirsch 1996). As such, we found that Least Terns and Piping Plovers generally avoided nesting close to predator perches and wooded areas, likely to reduce the risk of predation, and similar results have been reported in previous studies (Sidle and Kirsch 1993, Kruse et al. 2001, U. S. Army Corps of Engineers 2011, Lott et al. 2013a,b). As also found in our study, Least Terns rarely nest within 150 m of shrubs, trees, or other features that provide perches for avian predators or wooded areas that may support mammalian predator communities along the Missouri River (U. S. Army Corps of Engineers 2011). Similarly, on the lower Platte, Niobrara, and Missouri rivers, nests of Least Terns and Piping Plovers were generally on sandbars where channels were ≥ 300 m wide (Platte River Recovery Implementation Program 2015b).

An important consideration for Piping Plover productivity is the relationship between nesting and foraging habitat (Cohen et al. 2009). When regulated by density-dependent factors such as territoriality and competition, species like Piping Plovers reach an equilibrium density determined by nesting and foraging habitat availability (Rodenhouse et al. 1997, Cohen et al. 2009, Catlin et al. 2015). Along the central Platte River, densities of Piping Plover breeding pairs at managed, off-channel sites averaged 0.77 pairs/ha (range = 0.42–1.09 pair/ha) and intraspecific territorial aggression was regularly observed (Keldsen and Baasch 2016). Based on breeding-pair counts and managed, off-channel habitat availability, we believe Piping Plovers were at a population equilibrium density along the central Platte River prior to 2009 and may currently be at an equilibrium density given that densities of breeding pairs have remained at 0.75–0.85 pair/ha (Keldsen and Baasch 2016).

Densities of Least Terns at managed, off-channel sites along the central Platte River averaged 2.25 pairs/ha from 2001 to 2015. This estimate is higher than some, but much lower than other, reported nesting densities (range = 0.6 pair/ha – 100 pair/ha; Archibeque 1987, Hill 1993, Hillman et al. 2013). Thompson et al. (1997) and Meduna (2006) reported that colonies typically consist of ≤ 25 pairs, which is similar to colony sizes at off-channel sites along the central Platte River. Given their colonial behavior, the magnitude of differences in reported nest densities, and the fact they have not been determined to be at carrying capacity or limited by any factor in other areas within their range, determining if Least Terns were at an equilibrium density on central Platte River, off-channel nesting habitat is difficult. However, trends between numbers of breeding pairs of Least Terns and habitat availability suggest that the population was at an equilibrium density prior to 2009 when construction began on additional off-channel habitat along the central Platte River. Recent breeding-pair counts have once again stabilized at a breeding-pair density of ~2 pairs/ha (Keldsen and Baasch 2016), providing further evidence that the population may have reached an equilibrium density for off-channel sites along the central Platte River.

Off-channel nesting habitat has been important for maintaining the presence of both Least Terns and Piping Plovers along the central Platte River (Sidle and Kirsch 1993, Keldsen and Baasch 2016). Habitat management at off-channel sites has been sufficient for maintaining high levels of productivity for Least Terns and Piping Plovers where more than two-thirds of their nests and broods were successful at the nine managed sites along the central Platte River from 2001 to 2015 (Platte River Recovery Implementation Program, unpubl. data). However, our results suggest additional measures such as removal of woody vegetation ≤ 150–200 m from nesting areas and specific site designs would increase the suitability of more of the nesting areas and the likelihood of additional nesting. An efficient site design for Least Terns would be circular, maximizing the area of nesting habitat away from the shoreline, whereas an effective site design for Piping Plovers would be more linear, maximizing the area of nesting habitat near the waterline. An efficient site design for both species would be lobate, incorporating centralized nesting habitat for Interior Least Terns and increased access to foraging areas for nesting and brood-rearing Piping Plovers.

Building on the current understanding of off-channel site utility for productivity, our results improve our understanding of how both Least Terns and Piping Plovers use off-channel sites for nesting and how physical site characteristics and inter- and intraspecific associations influence nest-site selection. To the extent that manipulation of these characteristics is possible, our results can be used to guide the creation and management of habitat to increase the potential for nesting throughout the range of both species.

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LITERATURE CITED

ARCHIBEQUE, A. M. 1987. Interior Least Terns nest on Sequoyah National Wildlife Refuge. U.S. Fish and Wildlife Service, Vian, OK.

ATWOOD, J. L., AND P. R. KELLY. 1984. Fish dropped on breeding colonies as indicators of Least Tern food habits. Wilson Bulletin 96: 34–47.

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 5: 4197–4209.

———, 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.

BEN-AKIVA, M. E., AND S. R. LERMAN. 1985. Discrete choice analysis: theory and application to travel demand. MIT press, Cambridge, MA.

BURGER, J. 1987. Physical and social determinants of nest-site selection in Piping Plover in New Jersey. Condor 89: 811–818.

———. 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. Wilson Bulletin 94: 531–545.

CATLIN, D. H., J. D. FRASER, AND J. H. FELIO. 2015. Demographic responses of Piping Plovers to habitat creation on the Missouri River. Wildlife Monographs 192: 1–42.

———, ———, ———, AND J. B. COHEN. 2011b. Piping Plover habitat selection and nest success on natural, managed, and engineered sandbars. Journal of Wildlife Management 75: 305–310.

COHEN, J. B., L. M. HOUGHTON, AND J. D. FRASER. 2009. Nesting density and reproductive success of Piping Plovers in response to storm- and human-created habitat changes. Wildlife Monographs 173: 1–24.

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. Cambridge University Press, Cambridge, UK.

DUCEY, J. 1981. Interior Least Tern (*Sterna antillarum athalassos*). U.S. Fish and Wildlife Service, Pierre, SD.

ELLIOTT-SMITH, E., AND S. M. HAIG. 2004. Piping Plover (*Charadrius melodus*). In: The Birds of North America (P. Rodewald, ed.). Cornell Lab of Ornithology, Ithaca, NY.

ESRI. 2011. ArcGIS Desktop: Release 10. Environmental Systems Research Institute, Redlands, CA.

FAANES, C. A. 1983. Aspects of the nesting ecology of Least Terns and Piping Plovers in central Nebraska. Prairie Naturalist 15: 145–154.

HASTIE, T. J., AND R. J. TIBSHIRANI. 1990. Generalized additive models. Chapman and Hall, London, UK.

HAYS, H., AND M. LECROY. 1971. Field criteria for determining incubation stage in eggs of the Common Tern. Wilson Bulletin 83: 425–429.

HILL, L. A. 1993. Status and distribution of the Least Tern in Oklahoma. Bulletin of the Oklahoma Ornithological Society 26: 1–24.

HILLMAN, D. H., S. M. KARPANTY, AND J. D. FRASER. 2013. Nest and breeding population abundance of Least Terns: assessing bias and variation in survey timing and methods. Journal of Field Ornithology 84: 287–298.

HOWLIN, S., W. P. ERICKSON, AND R. M. NIELSON. 2004. A validation technique for assessing predictive abilities of resource selection functions. In: Proceedings of the symposium on resource selection methods and applications (S. Huzurbazar, ed.), pp. 40–51. Omnipress, Madison, WI.

KELDSEN, K. J., AND D. M. BAASCH [online]. 2016. Platte River Recovery Implementation Program: 2016 Interior Least Tern and Piping Plover monitoring and research report for the central Platte River, Nebraska. <https://www.platteriverprogram.org/PubsAndData/ProgramLibrary/PRRIP%202016%20Tern%20and%20Plover%20Monitoring%20and%20Research%20Report.pdf> (Accessed 19 June 2017).

KIRSCH, E. M. 1996. Habitat selection and productivity of Least Terns on the lower Platte River, Nebraska. Wildlife Monographs 132: 3–48.

KOLBE, J. J., AND F. J. JANZEN. 2002. Impact of nest-site selection on nest success and nest temperature in natural and disturbed habitats. Ecology 83: 269–281.

KOTLIAR, N. B., AND J. BURGER. 1986. Colony site selection and abandonment by Least Terns (*Sterna antillarum*) in New Jersey, USA. Biological Conservation 37: 1–21.

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.

LE FER, D., J. D. FRAZER, AND C. D. KRUSE. 2008. Piping Plover foraging-site selection on the Missouri River. Waterbirds 31: 578–592.

LEEPER, T. J. [online]. 2017. Interpreting regression results using average marginal effects with R's margins. <ftp://cran.r-project.org/pub/R/web/packages/margins/vignettes/TechnicalDetails.pdf> (Accessed 1 June 2017)

LOEGERING, J. P., AND J. D. FRASER. 1995. Factors affecting Piping Plover chick survival in different brood-rearing habitats. Journal of Wildlife Management 59: 646–655.

LONG, J. S., AND J. FREESE. 2006. Regression models for categorical dependent variables using strata, 2nd ed. StrataCorp LP, College Station, TX.

LOTT, C. A., S. F. RAILSBACK, C. J. R SHEPPARD, AND M. C. KOOHAFKAN [online]. 2013a. Developing and testing TernCOLONY 1.0: an individual-based model of Least Tern reproduction. U.S. Army Corps of Engineers, Washington, D.C. <http://www.dtic.mil/docs/citations/ADA587603> (Accessed 19 June 2017).

———, R. L. WILEY, R. A. FISCHER, P. D. HARTFIELD, AND J. M. SCOTT. 2013b. Interior Least Tern (*Sternula antillarum*) breeding distribution and ecology: implications for population-level studies and the evaluation of alternative management strategies on large, regulated rivers. Ecology and Evolution 3: 3613–3627.

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, Dordrecht, The Netherlands.

MASLO, B., J. BURGER, AND S. N. HANDEL. 2012. Modeling foraging behavior of Piping Plovers to evaluate habitat restoration success. Journal of Wildlife Management 76: 181–188.

———, S. N. HANDEL, AND T. POVER. 2011. Restoring beaches for Atlantic Coast Piping Plovers (*Charadrius melodus*): a classification and regression tree analysis of nest-site selection. Restoration Ecology 19: 194–203.

MCFADDEN, D. 1978. Modeling the choice of residential location. In: Spatial interaction theory and planning models (A. Karlquist, ed.), pp. 79–96. North Holland Publishing Company, Amsterdam, The Netherlands.

MEDUNA, L. R. 2006. Population status, breeding biology and habitat selection of Interior Least Terns (*Sterna antillarum athalassos*) on the Red River, Arkansas. M. S. thesis, Arkansas Tech University, Russellville, AR.

PATTERSON, M. E. 1988. Piping Plover breeding biology and reproductive success on Assateague Island. M.S. thesis, Virginia Polytechnic Institute and State University, Blacksburg, VA.

———, J. D. FRASER, AND J. W. ROGGENBUCK. 1991. Factors affecting Piping Plover productivity on Assateague Island. Journal of Wildlife Management 55: 525–531.

PLATTE RIVER RECOVERY IMPLEMENTATION PROGRAM [online]. 2012. PRRIP tern and plover minimum habitat criteria. <https://www.platteriverprogram.org/PubsAndData/ProgramLibrary/PRRIP%202012_LTPP%20Min%20Habitat%20Criteria_Draft.pdf> (Accessed 19 April 2017).

———. 2015a. PRRIP 2015 Central Platte River tern and plover monitoring and research protocol. <https://www.platteriverprogram.org/PubsAndData/ProgramLibrary/2015%20PRRIP%20Tern%20and%20Plover%20Monitoring%20and%20Research%20Protocol.pdf> (Accessed 8 June 2017)

———. 2015b. Interior Least Tern (*Sterna antillarum athalassos*) and Piping Plover (*Charadrius melodus*) habitat synthesis chapters. <https://www.platteriverprogram.org/PubsAndData/ProgramLibrary/PRRIP%202015_Tern%20and%20Plover%20Habitat%20Synthesis%20Chapters.pdf> (Accessed 20 June 2017)

PRINDIVILLE-GAINES, E. P., AND M. R. RYAN. 1988. Piping Plover habitat use and reproductive success in North Dakota. Journal of Wildlife Management 52: 266–273.

R DEVELOPMENT CORE TEAM. 2015. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

RODENHOUSE, N. L., T. W. SHERRY, AND R. T. HOLMES. 1997. Site-dependent regulation of population size: a new synthesis. Ecology 78: 2025–2042.

SCHWEITZER, S. H., AND D. M. LESLIE, Jr. 1996. Foraging patterns of the Least Tern (*Sterna antillarum*) in north-central Oklahoma. Southwestern Naturalist 41: 307–314.

SHERFY, M. H., M. J. ANTEAU, T. L. SHAFFER, M. A. SOVADA, AND J. H. STUCKER [online]. 2012a. Foraging ecology of Least Terns and Piping Plovers nesting on central Platte River sandpits and sandbars. U.S. Geological Survey Open-File Report 2012–1059. <https://www.platteriverprogram.org/PubsAndData/ProgramLibrary/USGS%202012_Foraging%20Habits%20of%20LTPP%20Report_Final.pdf> (Accessed 1 June 2017).

———, J. H. STUCKER, AND M. J. ANTEAU. 2008. Missouri River emergent sandbar habitat monitoring plan: a conceptual framework for adaptive management. U.S. Geological Survey Open-File Report 2008–1223, Jamestown, ND.

———, ———, AND D. A. BUHL. 2012b. Selection of nest-site habitat by Interior Least Terns in relation to sandbar construction. Journal of Wildlife Management 76: 363–371.

SIDLE, J. G., D. E. CARLSON, E. M. KIRSCH, AND J. T. DINAN. 1992. Flooding: mortality and habitat renewal for Least Terns and Piping Plovers. Colonial Waterbirds 15: 132–136.

———, AND E. M. KIRSCH. 1993. Least Tern and Piping Plover nesting at sand pits in Nebraska. Colonial Waterbirds 16: 139–148.

SPEAR, K. A., S. H. SCHWEITZER, R. GOODLOE, AND D. C. HARRIS. 2007. Effects of management strategies on the reproductive success of Least Terns on dredge spoil in Georgia. Southeastern Naturalist 6: 27–34.

STUCKER, J. H., D. A. BUHL, AND M. H. SHERFY. 2012. Emergent sandbar construction for Least Terns on the Missouri River: effects on forage fishes in shallow-water habitats. River Research and Applications 28: 1254–1265.

THOMPSON, B. C., J. J. JACKSON, J. BURGER, L. A. HILL, E. M. KIRSCH, AND J. L. ATWOOD. 1997. Least Tern (*Sterna antillarum*). In: The Birds of North America (P. Rodewald, ed.). Cornell Lab of Ornithology, Ithaca, NY.

U. S. ARMY CORPS OF ENGINEERS. 2011. Final programmatic environmental impact statement for the mechanical and artificial creation and maintenance of emergent sandbar habitat in the riverine segments of the upper Missouri River. U. S. Army Corps of Engineers, Omaha, NE.

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, Boca Raton, FL.