

Sandbars Managed for Least Terns within the Missouri River: Evaluating the
Influence of Fish, Spatial Scale, and Environment on Habitat Use

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Abstract

Interior Least Terns (*Sternula antillarum*) nest on barren sandy habitats, typically sandbars and shorelines within large river systems of the central United States. Loss of natural ecosystem processes which create and maintain these habitats is considered the primary reason for population decline and Federal listing of this population. Throughout their range, management for Least Terns focuses on maintenance of breeding habitats, including placement of dredged material specifically as nesting substrate. Wide expanses of barren land are known to attract Least Terns, yet specific small scale habitat features are thought to trigger nest habitat selection. Yet as a plunge-diving piscivore, Least Terns also rely on ready access to appropriately sized slender-bodied fish: <52 mm total length for adults and <34 mm total length for young chicks. It remains unknown whether sandbar construction is a benefit or a detriment to forage abundance for Least Terns. Lastly, the relationship between availability of nesting habitats and required foraging habitats remains ambiguous. This information is needed to refine understanding of Least Tern habitat needs from a foraging ecology perspective, and contribute to knowledge and potential value of habitat restoration efforts. This study evaluates 1) the shallow water (<1.5 m) fish community near river and mechanically created emergent sandbars during three nesting seasons (2006-2008), 2) nest-scale habitat selection to determine if nest habitats differ between constructed and natural sandbars, and it evaluates the consequences of this selection on nest success, and 3) the potential associations between specific habitat features, at differing spatial scales, associated with airborne and foraging Least Terns. The research effort focused on the 95 kilometers of Gavins Point Reach of the Missouri River, between Yankton, SD and Ponca, NE during the Least Tern nesting season in 2006-2008. We sampled fish within 15-16 areas every two weeks from late May - July to document the relative abundance, species richness, and size classes of fish. Using systematic surveys on sandbars every 2-3 days, we detected and tracked 869 Least Tern nests until eggs hatched or failed, on constructed

and natural sandbars in the Missouri River examining them for evidence of microhabitat selection at the nest and 3 m from nest. Least Terns successful foraging sites ($N=416$) were compared to a paired nearby random location to evaluate evidence of habitat selection during successful foraging in 2007-2008. We used systematic surveys every two weeks from late May - July in each year to identify Least Tern airborne (foraging or flying) locations within the river corridor (2006:966 sites, 2007:2940 sites, 2008:2003 sites), recording them using spot mapping. We modeled the probability that an observation (random and bird) as an airborne tern using logistic regression and habitat variables derived from remote sensing. Lastly, to refine our understanding of behavior in specifying habitat use, we modeled the probability of a location as a foraging site.

Fish relative abundance was negatively related to depth. Catches were dominated by schooling species, including emerald shiner, sand shiner, spotfin shiner, and bigmouth buffalo. Significant inter-annual differences in relative abundance were observed, with generally increasing trends in intra-seasonal relative abundance of shiners and the smallest size classes of fish (<34 mm). Significant differences in the fish communities between the sandbar types were not detected in this study. These results suggest that mechanical sandbar habitats host comparable fish communities at similar levels of relative abundance.

Among nests, significant differences were observed in substrates, amount of debris, and measures of vegetation between natural and created habitats, and between microhabitat at nests and the surrounding area. In general, Least Tern nest sites had coarser and larger substrate materials at the nest, more debris, and shorter and less vegetation compared to areas within the 3 m surrounding area. Nests in constructed habitats had a greater proportion of coarse substrates and less vegetation or debris than naturally created habitats. Observed nest success among constructed sandbars was 1.8x greater than that recorded among nests on natural sandbars, but a greater proportion of nests on natural bars were in or adjoining moist habitats where they were frequently destroyed. The best supported model predicting nest success on

constructed and natural sandbars each included positive associations with percentage of pebble substrate, but inclusion of additional habitat predictors differed by sandbar type. Selection of microhabitat characteristics at the nest and vicinity constrains this species to barren water and wind scoured habitats. Historically, scoured habitats and the comparative abundance of debris within sites may have been a cue indicating safe habitats as river stage decreased. Water management regimes during this study favored survival of nests on higher elevation sandbars which included limited areas of wet substrates, typical of mechanically constructed sandbars.

Among the micro-site habitat assessments for foraging birds, differences were not observed in water depth availability between natural or mechanically created habitats. Based on AIC relative importance scores, the variables water depth and microhabitat characteristics were most critical among micro-site characteristics of successful foraging locations; turbidity and larger scale aquatic features were comparatively of less importance. Within the greater landscape, Least Tern airborne locations within the river corridor were best explained by multi-scale logistic regressions; birds concentrated in areas with higher proportions of sandbar and wet sand habitats (200 m radius), while avoiding trees (50 m radius). When applied to a reserved sample of random locations, results suggest that in any given year, 40-97% of river corridor habitats were likely unsuitable for airborne terns. Furthermore, habitat use differed by behavior; foraging birds approached nearer to wet sand patches and in areas with less emergent sandbar habitat than flying birds, with some habitat relationships differing by year. Despite the surficial visual uniformity of many aquatic habitats on the Missouri River, successful foraging by Least Terns was associated with shallow, slack-water microhabitats adjacent to emergent sandbars and within areas with a greater proportion of sandbar habitat. This study demonstrates the importance of incorporating both spatial scale and behavior into ecological assessments of Least Tern foraging habitats.

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Preface

The Missouri River is one the longest rivers in North America, winding >2,500 miles across 7 states, from the Rocky Mountains of Montana and Wyoming in the west, to its confluence with the Mississippi River in Missouri in the east. Beginning shortly after the Lewis and Clark expedition of 1804-1806, the push for westward expansion moved upstream along the Missouri River as a primary route of travel and source and avenue of commerce. With its shifting sandy channel, early explorers and travelers documented repeatedly the hazards to navigation: shallow depth, numerous sandbars, copious trees and organic debris in the river, and regular flooding. Shortly after western settlements began, efforts were initiated toward controlling the Missouri River: stop the flooding, remove and minimize navigation hazards, and harness the river's resources to promote commerce. The first efforts began in the 1830s with Congress authorizing removal of trees and snags to promote safe navigation. Throughout the 19th - 20th century successive endeavors and regular large-scale floods culminated in Congress passing the Flood Control Act of 1944, ushering in the Pick-Sloan era. From 1933 – 1957, the US Army Corps of Engineers completed the construction of six major main-stem dams across the Missouri River, in Montana, North Dakota, and South Dakota. The purpose of these dams was to provide the nation multiple benefits, through the Flood Control Act's eight authorized purposes: flood control, hydropower, irrigation, recreation, water supply, navigation, flood control, and fish and wildlife. Today, primary operational control of the river

remains with the Army Corps of Engineers, and while management remains focused on those original authorized purposes, efforts are tempered by modern requirements including subsequently enacted federal environmental law, including National Environmental Policy Act (NEPA) of 1970, and the Endangered Species Act (ESA) of 1973.

Since the closure of the Gavins Point Dam in 1957, declines were documented in the quality of the river ecosystem, and species depending on it. Three species with dependence on the Missouri River environment became the focus of habitat and population mitigation efforts after their federal listing for protection under ESA: Pallid Sturgeon (*Scaphirhynchus albus*), Piping Plover (*Charadrius melodus*) and Least Tern (*Sternula antillarum*). The focus of river management for the birds changed with the release of the *2003 Amendment to the 2000 Biological Opinion on the Missouri River Main Stem Reservoir System, Operation and Maintenance of the Missouri River Bank Stabilization and Navigation Project, and Operation of the Kansas River Reservoir System* (USFWS 2003) from a strategy of management through river flow manipulation, to one where habitat objectives were met through mechanical means.

In 2005, I was assigned with serving as a lead researcher on a project led by Northern Prairie Wildlife Research Center (Dept of Interior, USGS) to evaluate if the habitat management efforts, as implemented, were a benefit to Least Terns. This study was one of several initiated simultaneously by Northern Prairie Wildlife Research Center (NPWRC) on Least Terns and Piping Plovers on the Missouri River.

The initial study design sought to connect observed habitat differences to changes in behavior, foraging, and reproductive success, while developing a better ecological understanding of Least Terns requirements.

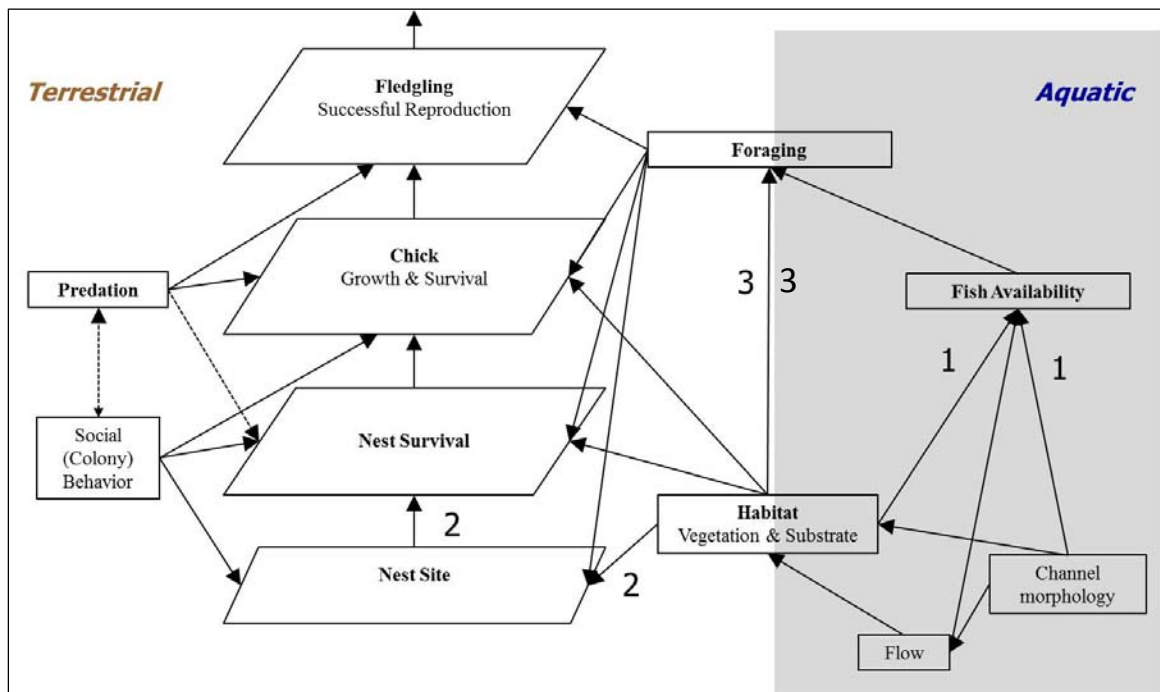


Figure 1. A Least Tern conceptual ecological model focused on nesting season requirements for suitable nest habitat (terrestrial) and foraging habitat (aquatic). Numbers (1-3) indicate the relationships explored within each dissertation chapter. Boxes indicate states and/or physical locations, while arrows indicate direction of stress or progress on state.

Using a conceptual ecological model (Figure 1), I began to systematically test our understanding of the relationships between Least Terns and their environment. From the scope of the entire Least Tern research effort, this dissertation examines three specific areas: 1) the availability of small fish and the habitat features associated

with where fish occur; 2) the influences of fine scale nest habitat and habitat selection on nest fate; and 3) an evaluation of the habitats Least Terns move through while airborne, and features of successful foraging locations. These three chapters are presented as manuscripts ready for submission to journals for peer review, with the first chapter, *Emergent Sandbar Construction For Least Terns On The Missouri River: Effects On Forage Fishes In Shallow Water Habitats*, published in April 2011. While I maintained my role as primary author of each manuscript, co-authors provided additional support as follows: Deb Buhl, consulting statistician on chapter 1 and 2; Larry Strong, preparation of landcover data from remote sensing imagery, chapter 3; and Mark Sherfy as co-principal investigator and Missouri River research team lead, chapters 1-3. The fourth chapter is a brief commentary from a broader perspective on the future of Least Terns, river management and science.

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Chapter 1.

EMERGENT SANDBAR CONSTRUCTION FOR LEAST TERNS ON THE MISSOURI RIVER: EFFECTS ON FORAGE FISHES IN SHALLOW WATER HABITATS

Emergent sandbars on the Missouri River are actively managed for two listed bird species, piping plovers and Interior least terns. As a plunge-diving piscivore, endangered least terns rely on ready access to appropriately sized slender-bodied fish: <52 mm total length for adults and <34 mm total length for young chicks. As part of a multi-agency recovery program, aimed at enhancing nesting habitat for plovers and terns, the U.S. Army Corps of Engineers mechanically created several emergent sandbars on the Missouri River. However, it was unknown whether sandbar construction is a benefit or a detriment to forage abundance for least terns. Therefore, we studied the shallow water (<1.5 m) fish community near river and mechanically created emergent sandbars during three nesting seasons (2006-2008). We sampled every two weeks each year from late May - July within 15-16 areas to document the relative abundance, species richness, and size classes of fish. Fish relative abundance was negatively related to depth. Catches were dominated by schooling species, including emerald shiner, sand shiner, spotfin shiner, and bigmouth buffalo. Significant inter-annual differences in relative abundance were observed, with generally increasing trends in intra-seasonal relative abundance of shiners and the smallest size classes of fish (<34 mm). Significant differences in the fish communities between the sandbar types were not detected in this study. Results suggest that mechanical sandbar habitats host comparable fish communities at similar levels of relative abundance. Further analyses are required to evaluate if the levels of fish relative abundance are adequate to support least tern foraging and reproduction.

Within expansive river systems of mid-continent North America, large sandbars provide essential habitats (e.g. foraging, nesting, resting) for a variety of bird species during migration and the breeding season. During the twentieth century, substantial alteration of the Missouri River, particularly closure of dams, bank stabilization and channelization (Galat *et al.*, 2005) resulted in loss of aquatic (submerged) and terrestrial sandbar habitats. Throughout the Missouri River system, but particularly in the lowest ~1,200 riverkilometers (RKM) and channelized portion of the river, declines in abundance and distribution were documented in small-bodied fish species requiring shallow-water habitats (Berry *et al.*, 2004). Recent research has evaluated the aquatic terrestrial interface concept (Junk *et al.*, 1989) within the context of the Missouri River (Reeves, 2006; Ridenour, 2007; Ridenour *et al.*, 2009; Tracy-Smith *et al.*, 2011). These efforts have concentrated on early life-stages of fish species, ontogenic associated habitat shifts, and the juxtaposition of these features to sandbars, bank lines, and channels (Reeves, 2006; Ridenour *et al.*, 2009). Earlier research on the shallow water areas adjacent to sandbars of the Mississippi documented habitat richness, species richness and greater relative abundance compared to deeper channel habitats (Tibbs and Galat, 1998). Broadly, there is an emerging understanding of the complexity of varying habitat niches within the aquatic terrestrial interface for species, throughout their life including fish (Reeves, 2006; Ridenour *et al.*, 2009), turtles and migrating birds (Tracy-Smith *et al.*, 2011).

Along the Missouri River, and elsewhere within the US Great Plains, terrestrial emergent sandbars are important nesting habitat for two federally listed

bird species, piping plovers (*Charadrius melodus*) and Interior least terns (*Sternula antillarum*). The Missouri River channel between Gavins Point Dam and Ponca State Park (RKM1306 – RKM1213, referred to as the “Gavins Point Reach” in this paper) retains some characteristics of the once braided-anastomosed river (Elliott and Jacobson 2006), including emergent (e.g. exposed from water) and submerged sandbars. The U. S. Army Corps of Engineers seeks to maintain and provide emergent sandbars specifically as nesting habitats for these two species under requirements of a Biological Opinion concerning operation of the Missouri River (U.S. Fish and Wildlife Service 2003). Most recently, management has focused on mechanically constructing emergent sandbars for nesting birds through placement of sediments from the riverbed or backwater restoration efforts. Least terns need emergent sandbars for nesting, but also require forage fish from nearby river habitats to feed themselves and their semi-altricial offspring. Within one of the Missouri River’s most active Least Tern nesting areas, the Gavins Point Reach, shallow water habitat acres have declined by ~60% (U.S. Fish and Wildlife Service; 2003), habitats in which most least tern forage fish are believed to be found. On the Mississippi River, shallow water habitats adjacent to least tern sandbars had greater species richness and fish catch per unit volume than deeper areas (Tibbs and Galat, 1998). Least terns forage near their colonies on the Platte River (0.1 km to 1.5 km, NE (Faanes 1983; Wilson *et al.*, 1993)), and ≤ 12 km from colonies at Salt Plains, OK (Schweitzer and Leslie, 1996). Based on unconsumed fish dropped in colonies in the central USA, narrow-bodied fish species likely dominate diets (*e.g.* shiners, minnows,

shad, killifish, chubs) (Schweitzer and Leslie, 1996; Thompson *et al.*, 1997; Wilson *et al.*, 1993). Rejected fish frequently included those with spines, body depths >1.5 cm, and lengths >9 cm (Thompson *et al.* 1997). Chicks will reject fish if too large for consumption (Massey *et al.*, 1992), and adults present smaller sized fish (<2 cm) are to chicks <3 days age (Schweitzer and Leslie, 1996). Lack of adequate nearby fish to support the colony, or appropriate sized prey for young chicks, has direct impacts on least tern adults and chicks through decreased egg size, reduced clutch size, increased nest abandonment, decreased chick growth and chick survival (Atwood and Kelly, 1984; Dugger, 1997; Massey *et al.*, 1992). But, few studies have evaluated least tern nesting habitat selection or assessed productivity while concurrently measuring aquatic resources directly (Tibbs and Galat, 1998), and for species with capacity to travel some distance to forage on fish, estimating “local” availability to food is challenging (Erwin, 1977; Fraser, 1997; Monaghan *et al.*, 1989). If management focuses on providing sandbar habitat for enhancing reproduction, but successful reproduction requires terrestrial and aquatic habitats, then consequence of management action on associated aquatic terrestrial interface habitats should also be considered.

Consequently evaluating terrestrial sandbar habitat management as success or failure in this situation may be tempered by a need to consider nearby aquatic prey availability, and possible prey responses to management. Construction of emergent sandbars changes the flow of the river and topography of its bed, thereby altering the composition of the forage fish community. The direction, duration and scale of such

alterations generally go unmeasured, although data from one Missouri River site (Mestl, 2004) suggested that the fish community and shallow water topography retained features consistent with the Gavins Point Reach (Galat *et al.* 2005). The substrate materials in this portion of the river are primarily sand, and as such, redistribute quickly and frequently. Fish within this rapidly shifting environment, and their associated food sources, may exhibit an acceptance or intolerance of disturbances, with the potential for exacerbation of existing degraded aquatic resource conditions.

This study was part of a greater comprehensive assessment of emergent sandbars, their habitats and influences on Interior least tern breeding season ecology. The objectives of this study were to: (1) assess if habitats adjoining river-created and mechanically constructed emergent sandbars retain similar fish communities throughout the least tern reproductive period (nesting through fledging), while (2) identifying which physical habitat characteristics (depth, turbidity, temperature, and sample location) best predict the shallow water prey fish community (e.g. relative abundance, species richness, and fish length size classes appropriate for least tern consumption). Following these analyses, the substrate composition and presence of fish were summarized.

METHODS

The study area included two adjacent areas of the Missouri River, the Gavins Point Reach (RKM1213 - RKM1292) and at the delta-lake transition of Lewis and

Clark Lake (RKM1331, 2007 only) (Figure 1). Sixteen sampling areas (Table 1) were established surrounding (bank to bank, and 0.8 RKM upstream and 0.8 RKM downstream) sandbars on which nesting least terns had been documented during the previous five years (G. Pavelka, U. S. Army Corps of Engineers, personal communication), or where new mechanically created sandbars were established for the birds in prior 6 months. Sampling areas were chosen so that they did not overlap and were geographically dispersed within the Gavins Point Reach, from just upstream of the James River confluence with the Missouri (RKM1291) to Ponca State Park (RKM1213). One sampling area, RKM1331, was added in 2007 following construction of new emergent sandbar unit, but it was excluded from sampling in 2008 for logistical reasons. Within each of the 16 delineated sampling areas, >300 random points were allocated to aquatic habitats between the Missouri River banks using ArcMap (ESRI). We assigned a unique number to each point, and visited them sequentially for sampling through the study; points were sampled without replacement throughout the study period. A sampling point was discarded and the next sequential point located for sample collection if (1) the random point was currently above the water (terrestrial), or (2) the water depth was >1.3 m at the sampling location, or (3) if a trawl was compromised during data collection (e.g. inversion or stuck on debris). Fish sampling was conducted during five sampling periods, every 2 weeks (hereafter, period) between June and August of 2006 – 2008 for the duration of the tern reproductive period; sampling for all areas within a period was conducted in ≤ 3 days to limit within-period variability due to discharge and

habitat conditions. The initiation of fish sampling each year coincided with the return of least terns to the study areas, with periods 1-2 during nest initiation and incubation, periods 3-4 during hatching and early chick rearing, and period 5 during late chick rearing and fledging. All sampling was conducted during daylight hours, 0900-1800H CST, avoiding crepuscular periods. Thus, for each year (3), at each area (15-16 sampling areas), in each sampling period (5 periods), a sample (three random 100m trawls) was collected.

We deployed an active sampling gear, the mini-Missouri trawl with 2.18 mm delta-style mesh in order to collect a standardized sample (volume), while maximizing capture of small-bodied fishes (*see Herzog et al., 2009* for additional trawl specifications). Trawl mesh materials had been treated with green dip latex coating. The trawl samples 2.16 m² area (width: 2.4 m, depth: 0.9 m) of the water column and has a weighted lower leading edge of the net to ensure constant contact with the substrate. All trawl gear was rigged identically. Each trawl was conducted by manually walking dragging the mini-Missouri gear downstream for 100m (2-3 min), at a pace slightly faster than the current so that otter boards were fully deployed, but not so fast as to induce back wash due to mesh size. Trawl distance (100m) was fixed using a known length line. Therefore sampling volume within each sampling period, by location, was ~648 m³ (3 trawls x 216 m³). At conclusion of each trawl, the catch was processed immediately, and most fish were released alive. During processing, fish were identified to species (Bailey and Allum, 1962; Becker, 1983; Cross and Collins, 1995; Morris *et al.*, 1974; Pflieger, 1991), measured

for total length (TL) (nearest mm), and photographed for reference and as vouchers. Deceased fish and those of unknown identification were retained for later species verification. For each sampling event, turbidity (Hach 2100P, NTU), and water temperature (standard liquid thermometer, °C) were measured at the trawl's starting point, and water depth (measuring rod, nearest 0.1 m) at the start and end of trawl. Substrate materials were qualitatively described throughout the trawling area following Missouri River standard sampling procedures (Drobish 2006).

Analysis

Fish sampling data were analyzed to examine differences between emergent sandbar types (river and mechanically created), while accounting for depth, turbidity, and temperature. As the gear was standard for all sampling, with approximately the same volume of river sampled, the resulting counts of fish relative abundance pooled across three subsamples (by period and location) were used in the analysis. We summarized response variables including: count of fish captured, number of species captured (richness), count of shiners captured, and count of fishes in 5 different size categories (Table 2). The size categories follow those consumed by least terns, and were delineated according to least tern bill length of 26 mm (Thompson et al. 1997); bill length confirmed in Oklahoma (Schweitzer and Leslie 1996), and by Stucker (*unpublished USGS data*) for our study area. We subsequently combined size classes 0 and 1 due to a large number of zeros. Prior to analyses, all response variables, except species count, were $\ln(y+1)$ transformed. River mile, turbidity, depth, and temperature were included in the models as continuous covariates; turbidity was log

transformed prior to analyses to reduce the effect of a few large values. We assigned a depth measurement to each trawl using the average of measurements obtained at its start and end point.

Statistical analyses were conducted using a strip-plot design, with sampling area of river being the experimental unit for emergent sandbar type (i.e., river or mechanically created), and year and periods the strips in the strip-plot model.

Covariate relationships to response variables were evaluated individually (Milliken and Johnson, 2002) to determine which covariates were significantly related to the response variable and the correct form (i.e., same or different slopes needed for each habitat type, year, or sampling period) of that relationship. Covariates were examined one at a time because small sample sizes did not allow for testing of four covariates simultaneously. Once the correct form of the covariate was determined, the strip-plot model was run including any significant covariates. Analyses were conducted using the mixed models procedure of SAS (SAS, 2007). Least squares means and differences of least squares means were examined for significant ($P < 0.05$) main effects or interactions, while adjusting for the effect of depth on the response variable. Results are presented as natural log mean with standard errors (SE), and a back-transformed mean, as appropriate.

RESULTS

We captured 10,015 fish from 230 samples between 2006-2008. Eighty percent (8,060 fish) were identified to species and an additional 5% to genus; <15% of fish

were unidentified, and these individuals primarily represented young-of-year (YOY) fish from two samples. We captured 35 fish species, including 10 shiner species from 4 genera (*Cyprinella* [2], *Notropis* [6], *Notemigonus* [1], *Luxilus* [1]) (Table 4). The most abundant fish species captured was bigmouth buffalo (*Ictiobus cyprinellus*) comprising 23% of the total catch, primarily from the aforementioned YOY catch. Other species encountered consistently included emerald shiner (*Notropis atherinoides*, 20%), sand shiner (*N. stramineus*, 9%) and spotfin shiner (*Cyprinella spiloptera*, 8%).

All Gavins Point Reach sampling areas yielded observations of at least 11 species in 3 years of sampling. The Lewis & Clark Lake sampling area yielded 9 fish species during 2007, with all species at this site being observed also downstream within the Gavins Point Reach. The greatest number of species (25) was observed at RKM1292, with 23 observed at RKM1234, and five sampling sites yielding 20 species each (RKM1215, 1225, 1230, 1273, and 1279). At three locations, RKM1230, 1234, and 1242, we captured 8 of the 10 shiner species; at the Lewis & Clark Lake site (RKM1331) we captured the fewest, 2 species, emerald shiner and river shiner (*N. blennioides*). Two shiner species, common (*Luxilus cornutus*) and golden (*Notemigonus crysoleucas*), were captured the least and encountered at 2/15 and 1/15 sampling sites, respectively, on the Gavins Point Reach. Silver chub (*Macrhybopsis storeriana*) was observed infrequently, but captured at 8 of 15 sampling sites within the Gavins Point Reach. Flathead chub (*Platygobio gracilis*) was the only other chub species observed, and it was captured at three sites, downstream of RM1225.

Trawl locations where fish were captured and those where no fish were captured had substrates dominated by sand. But among subsamples yielding fish (415 of 696), substrates averaged 17% silt concentration, with 38% (156 of 415) having silt; 28% had coarse or fine organic material. Trawls without fish (281 of 696 subsamples) averaged 8% silt concentration, with 21% (60 of 281) having silt; 18% had coarse or fine organic material. Within the combined samples, water temperatures generally increased through the season, with samples averaging 21° C in May and 26° C in late July (Figure 2). Turbidity varied by period and year, ranging between 25 and 60 NTU, except in 2008 when elevated readings were associated with James River flooding (Figure 2). Temperature, turbidity and river kilometer location were not included in final models as none was associated with measures of fish relative abundance or richness.

Responses of the fish measures primarily demonstrated consistency in results. Water depth (Figure 3) was a primary explanatory factor, while an effect of emergent sandbar type was not observed for any fish response. Inter-annual variability (Figure 4) was observed for most measures, and the smallest fish size class 0-1 demonstrated intra-seasonal variability (Figure 5). Below, details for each fish response are presented.

Count of Fish Captured. The total number of fish captured, relative abundance, was negatively related to depth (Figure 3), and this relationship was the same for all combinations of emergent sandbar type, year, and period. After accounting for average depth, significant differences were detected among years ($F_{2,23} = 3.39$, $P =$

0.05) (Figure 4), but not between emergent sandbar types ($F_{1,16} = 0.31, P = 0.59$) (Table 5) or among periods ($F_{4,64} = 0.85, P = 0.50$). No significant interaction effects were detected (all $P > 0.47$). The number of fish caught in 2006 was significantly less than in 2007 ($P = 0.02$), but not 2008 ($P = 0.27$); 2007 did not differ significantly from 2008 ($P = 0.12$) (Figure 4).

Species Captured. The number of species captured per sampling area was related to the average depth, and this relationship differed by period. For periods 2, 3, and 5, the relationship between number of species and depth was significantly negative; for periods 1 and 4, the relationship was not significant. After accounting for depth, significant differences were detected among years ($F_{2,23} = 6.96, P < 0.01$) and periods ($F_{4,64} = 6.57, P < 0.01$), but not between emergent sandbar types ($F_{1,16} = 0.03, P = 0.86$); no significant interaction effects were detected (all $P > 0.10$). The number of species per trawl captured in 2007 (4.6(0.4)) was significantly greater than in 2006 (2.4(0.5)) ($P < 0.01$) and 2008 (3.2(0.4)) ($P = 0.02$), but not between 2006 and 2008 ($P = 0.20$).

Shiners Captured. The count of shiners captured was negatively related to the average depth (Figure 3), and this relationship was the same for all combinations of emergent sandbar type, year, and period. After accounting for average depth, significant differences were detected among years ($F_{2,23} = 6.47, P = 0.01$) (Figure 4) and time periods ($F_{4,64} = 2.75, P = 0.04$) (Figure 5), but not between emergent sandbar types ($F_{1,16} = 0.32, P = 0.58$). No significant interaction effects were detected (all $P > 0.26$). The total number of shiners caught in 2006 was significantly

less than in 2007 ($P < 0.01$); marginally significant differences were detected between 2006 and 2008 ($P = 0.06$) and between 2007 and 2008 ($P = 0.08$). Significantly fewer shiners were captured in periods 2, 3, and 4 than in week 5 ($P < 0.02$).

Number of Fish of Size Class 0 – 1. The number of size class 0-1 fish captured was not related to any of the covariates included in the analysis. Significant differences were detected among periods ($F_{4,64} = 3.67$, $P = 0.01$) (Figure 5), and marginally significant differences were detected among years ($F_{2,23} = 3.18$, $P = 0.06$) (Figure 4), but no significant differences were detected between emergent sandbar types ($F_{1,16} = 0.67$, $P = 0.43$). No significant interaction effects were detected (all $P > 0.16$). Significantly fewer fish of size class 0 - 1 were captured in time periods 1 and 2 than in periods 3 and 5 ($P < 0.05$) and significantly less in period 4 than period 3 ($P = 0.05$) (Figure 5).

Number of Fish of Size Class 2. The number of size class 2 fish captured was negatively related to depth (Figure 3), and this relationship was the same for all combinations of emergent sandbar type, year, and period. After accounting for depth, significant differences were not detected among years ($F_{2,23} = 2.74$, $P = 0.09$) (Figure 4), between emergent sandbar types ($F_{1,16} = 0.00$, $P = 0.95$) (Table 5), or among periods ($F_{4,64} = 1.98$, $P = 0.11$). No significant interaction effects were detected (all $P > 0.31$).

Number of Fish of Size Class 3. The total number of size class 3 fish captured was negatively related to depth (Figure 3), and this relationship was the same for all combinations of emergent sandbar type, year, and period. After accounting for depth,

significant differences were detected among years ($F_{2,23} = 7.40, P < 0.01$) (Figure 4), but not between emergent sandbar types ($F_{1,16} = 0.19, P = 0.67$) (Table 5) or among periods ($F_{4,64} = 0.83, P = 0.51$). No significant interaction effects were detected (all $P > 0.19$). The total number of fish in size class 3 caught in 2006 was significantly less than in 2007 ($P < 0.01$) and 2008 ($P = 0.01$), but significant differences were not detected between 2007 and 2008 ($P = 0.30$) (Figure 4).

Number of Fish of Size Class 4. The total number of size class 4 fish captured was negatively related to depth (Figure 3), and this relationship was the same for all combinations of emergent sandbartype, year, and period. After accounting for depth, significant differences were detected among years ($F_{2,23} = 6.10, P = 0.01$) (Figure 4), but not between emergent sandbartypes ($F_{1,16} = 0.59, P = 0.45$) (Table 5) or among periods ($F_{4,64} = 0.23, P = 0.92$). No significant interaction effects were detected (all $P > 0.37$). The total number of size class 4 fish caught in 2006 was significantly less than in 2007 ($P < 0.01$) and 2008 ($P = 0.01$), but significant differences were not detected between 2007 and 2008 ($P = 0.56$) (Figure 4).

DISCUSSION

Through the course of this assessment, we did not detect substantial differences in the shallow water prey fish community between river-created and mechanically constructed sandbars. Only one of the physical habitat predictors we tested, depth, appeared to predict fish relative abundance. However, we were unable to determine in a more comprehensive fashion, if physical habitat differed between emergent

sandbar types. While our study did not aim explicitly to explore physical habitat differences adjoining river and mechanically created emergent sandbar, it is important to note that where trawling efforts captured fish, fine and organic substrate materials were frequently present. Presence of fine substrate materials, including silt and organic particulates indicates areas of deposition, with comparatively slower velocity (Gordon *et al.*, 2004). Shallower waters are typically associated with reduced flow velocities, particularly on submerged bars adjacent to emergent sandbar habitats (Bowen *et al.*, 2003). Therefore, it is reasonable to believe that shallow water habitats adjoining emergent sandbar within the Gavins Point Reach likely exhibit aquatic physical microhabitat variability, consistent with previous studies (Bowen *et al.*, 2003; Tibbs and Galat, 1998).

The Gavins Point Reach of the Missouri River retains emergent sandbar and other geomorphically complex characteristics (Elliot and Jacobson, 2006), which would support maintenance of micro-scale habitat complexities. Within this existing diversity of habitats, addition of mechanical emergent sandbar may not provide specialized local habitat conditions for fish occupation which differ from those habitats found generally within the reach. Consequently, addition of emergent sandbar elsewhere may have a more profound impact on the local or reach community. For example, the sampling site on the reservoir had fewer species, but similar relative abundance per sample, to sites on the Gavins Point Reach. A recent study on this same reservoir, Lewis and Clark Lake, documented greater relative abundance of fish in areas of microhabitat variability (Kaemingk *et al.*, 2007). As

sampling on the reservoir was initiated after completion of emergent sandbar construction, it is not clear if its margins provided novel or expanded habitats. As emergent sandbar type was not a predictor of relative fish abundance in our samples, we were then able to explore what other factors predicted observed relative abundance measures. Habitat heterogeneity and within season timing of sampling were two areas of interest. The catch composition within shallow water habitats of the Gavins Point Reach was diverse and composed of species similar to previous studies (Berry *et al.*, 2004; Klumb, 2007; Mestl, 1994). Unlike prior studies in this same area though, our study clearly documents a strong negative relationship between depth and relative abundance of fish. On the Mississippi River, shallow water habitats adjoining least tern colonies had a greater abundance of fish than deeper water, and these areas also showed greater physical habitat variability (e.g. temperature, water clarity, current velocity, and substrate composition) (Tibbs and Galat, 1998).

Elsewhere, water depth is an important predictor of abundance (Gelwick *et al.*, 2001; Jowett *et al.*, 1996), but it may affect species and age-classes differently. Young fish have been documented to seek protection in shallow water, away from greater velocities found in deeper water (Barko *et al.*, 2004; Brown and Coon, 1994; Flore and Keckeis, 1998). Although this study did not see a negative relationship with depth for fish in size classes 0-1 (<34 mm), this study's catches may not have been adequate to detect this relationship. Areas of comparatively more shallow water, particularly in association with submerged bars adjacent to emergent sandbar

emergent sandbars, have reduced flow velocities (Bowen et al., 2003). Shallow water habitats found on channel edges and margins of emergent sandbars are important habitats for smaller bodied large-river fish species in the Missouri River (Ridenour *et al.*, 2009; Ridenour, 2007) and elsewhere (Barko *et al.*, 2004; Conklin *et al.*, 1995; Johnson and Jennings, 1998; Scheidegger and Bain, 1995; Van Steeter and Pitlick, 1998). As found with total relative abundance, size classes 2-4 were each negatively associated with depth. This relationship appears to be independent of year, period within the season, or the dominant emergent sandbar type within the sampled area. Similarly, Ridenour (2007) observed that the smallest (≤ 35 mm) fish were in depths 0.05 – 0.24 m, primarily emergent sandbar margins, whereas larger fish (35-105 mm) were captured in slightly deeper water (0.34-0.56 m).

Depth in our study is likely associated with changes in flow velocities. Within the Gavins Point Reach, Mestl (2004) reported seine sampling results adjacent to the RKM1215 emergent sandbar at water depths averaging 0.6 m depth, and flow velocities 0.11 m/s. Although flow velocities in this study were not consistently assessed, we can deduce that areas with fish typically had comparatively lower velocities based on the presence of silt and organic debris; silt materials averaged <2% in Mestl's sampling at RKM1215. Our observations of silt abundance suggest that habitats may accumulate fine materials in years following construction.

Generally, capture of fish was associated with presence of greater amounts of these fine sediments and organic debris.

While several of these correlated physical habitat measures may help explain fish relative abundance spatially, temporal changes in relative fish abundance as forage base are vital when considering the phenology of the least tern reproductive period. Intra-seasonal variability in relative abundance among the size class 0-1 and within shiners was detected in this study (Figure 5). This trend has been demonstrated previously during fish sampling on the Missouri River (Ridenour, 2007), the Mississippi River (Holland 1986), and in lotic systems adjacent Forster's tern colonies in Minnesota (Fraser, 1997). Prior predictions also suggest Least Tern nesting should occur on the descending limb of the flood hydrograph, when recent fish spawning will likely provide suitable prey concurrent with least tern hatching (Tibbs and Galat 1998). On the Mississippi, seasonal variation in YOY fish density is associated with seasonal patterns of increasing water temperature (Holland, 1986), a factor which may have been confounded with the time periods included in our analysis (*see* Figure 2). We documented generally increasing relative abundance in the catch of the smallest size fish (size 0-1, <33mm) through the sampling season, May – July. This period of time is coincident with fish recruitment and growth of YOY class, and demand for this size fish to feed young chicks. Reeves (2006) and Ridenour (2007) documented use of sandbar-channel margin slack-water by young fish in the lower Missouri, and in similar habitats on the Mississippi (Barko *et al.* 1994). Fish in size classes 0-3 (<52 mm) can be consumed by least terns, but only the smallest size classes of fish 0-1 (<34 mm) could be consumed by chicks in the first days and weeks of life. Fish of appropriate sizes must be available for successful

least tern reproduction (Atwood and Kelly, 1984; Dugger, 1997), and decreased food availability is associated with reproductive failure (Massey *et al.*, 1992).

Among species most abundant in these shallow water samples, small surface schooling species were notable, particularly emerald shiner, sand shiner, and spotfin shiners, species which should exhibit large pulses of annual recruitment, as observed in our analysis. In Oklahoma, Laura Hill reported least terns foraged at sites with greater densities of fish than random locations (Thompson *et al.*, 1997). If a greater abundance of prey stimulates tern foraging behaviors, then schools of fish in shallow water present an efficient target for foraging. Least terns capture fish from the surface of the water during aerial dives, and fish are vulnerable to capture within 15 cm of surface (Thompson *et al.*, 1997). As observed in our data, fish relative abundance for all size classes, except for size class 0-1 (<34mm), was greatest in the shallowest water. If fish relative abundance is greater in shallower water, then the fish density available for capture by foraging least terns also increases with decreasing depth. Observed successful foraging by least terns using shallow water habitats of the Gavins Point Reach (Stucker, *unpublished USGS analysis*) reiterates that these habitats are vital for terns and as habitats for small bodied fishes.

With widespread modification of flow regimes of rivers worldwide, particularly following dam construction, the dynamic flow conditions which maintain emergent sandbars and associated shallow water habitats have been dampened in frequency and magnitude (Poff *et al.* 2007). Results from this study are consistent with other studies that have also reported increased fish abundance in shallow water, although increases

in abundance by depth may be species specific (Gelwick et al., 2001; Jowett et al., 1996; Welker and Scarnecchia, 2004). Observed depth dependant relationships may be a consequence of specific habitat requirements, or limitations in habitat availability. However, any variation in the abundance of shallow water habitat between sandbar types could affect the overall availability of forage fish for least terns. Inference from relative abundance, as presented in this study, to overall abundance requires knowledge of proportions of river habitats present by depth. The historic Missouri River channel included an abundance of sandbars, and today the Gavins Point Reach retains some sandbars and comparatively complex geomorphic characteristics (Elliot and Jacobson, 2006) as compared to other areas of the channelized Missouri. Channel incision (U.S. Army Corps of Engineers, 1996), decreased sediment loads, and manipulated flows reduce the propensity of the river to retain areas of shallow water habitats (Jacobson and Galat, 2006). This study indicates that shallow water habitats associated with both river and mechanically constructed sandbars support similar fish communities of appropriate size for foraging least terns. While measures of the prey fish community are similar between habitats adjoining river and mechanically created sandbars, the correspondence between forage fish population and abundance of shallow water habitats at greater spatial scales (e.g. Gavins Point Reach) has not been evaluated. Subsequent analyses linking this study's measures of relative abundance to least tern foraging behaviors, movements, and chick survival will be essential for determining direct ecological significance of these findings for least terns.

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Table 1. Study site sampling locations, river mile and kilometer boundaries, and sandbar type for 2006 – 2008. Sandbar types are indicated by their creation type, R (river) and M (mechanical). Locations which were not sampled in a year are indicated by (-).

Site	River miles \	River kilometers	2006	2007	2008
	(RM)	(RKM)			
	Downstream -	Downstream –			
	Upstream	Upstream			
1331	825.6 - 827.6	1328.6 - 1331.8	-	M	-
1291	801.5 - 803.4	1289.8 - 1292.9	R	R	R
1284	797.7 - 799.6	1283.7 - 1286.8	R	R	R
1279	794.6 - 795.9	1278.7 - 1280.8	R	R	R
1276	792.5 - 794.3	1275.4 - 1278.3	R	R	R
1273	790.8 - 792.1	1272.6 - 1274.7	R	R	M
1268	787.3 - 789.5	1267.0 - 1270.5	R	R	R
1257	780.6 - 782.2	1256.2 - 1258.8	R	R	R
1250	776.8 - 778.1	1250.1 - 1252.2	R	R	M
1242	771.9 - 773.5	1242.2 - 1244.8	R	R	R
1239	769.1 - 770.8	1237.7 - 1240.4	M	M	M
1234	767.1 - 768.3	1234.5 - 1236.4	R	R	R
1230	764.0 - 765.1	1229.5 - 1231.3	R	R	R
1225	760.5 - 762.1	1223.9 - 1226.4	M	M	M

1221	758.2 - 759.7	1220.2 - 1222.6	R	R	R
1215	754.3 - 755.4	1213.9 - 1215.6	M	M	M

Table 2. Fish size class, fish body length (TL), and relationship with least tern bill length. Least tern bill length is estimated as 26 mm (Thompson et al. 1997).

Size Class	Fish length (TL,mm)	Relationship to least tern bill length
0	<20	< 1 bill
1	21 – 33	~ 1 bill
2	34 – 46	> 1 bill
3	47 - 52	2 bills
4	>52	> 2 bills

Table 3. Model parameters and response variables included in the evaluation

Parameter	Parameter Type	Description
Year	Design	2006, 2007, 2008
Period	Design	1 = late May; 5 = late July to early August
Type	Design	Emergent sandbar creation type, River <i>or</i> Mechanically Created
River kilometer	Covariate	Location of sampling area
Depth	Covariate	Average depth
Turbidity	Covariate	Average turbidity (ntu)
Temperature	Covariate	Average temperature at sampling location
Count of Fish	Response	Count of all fish in sample
Species	Response	Count of species captured
Shiners	Response	Count of shiner species (<i>Notropis</i> , <i>Notemigonus</i> , <i>Luxilus</i> , <i>Cyprinella</i>)
Size Class 0-1	Response	Count of all fish in size class 0-1
Size Class 2	Response	Count of all fish in size class 2
Size Class 3	Response	Count of all fish in size class 3
Size Class 4	Response	Count of all fish in size class 4

Table 4. Species and counts of fish captured using the mini-Missouri trawl during 15 sampling periods in 2006-2008 by sampling unit. Results represent total counts from 15 sampling periods across 3 years, except RKM1331 (5 sampling periods, 2007).

Scientific name	Common name	RKM segment															
		1331	1291	1284	1279	1276	1273	1268	1257	1250	1242	1239	1234	1230	1225	1221	1215
<i>Scaphirhynchus</i>	Shovelnose																
<i>platyrhynchus</i>	sturgeon																
<i>Lepisosteidae sp.</i>	Unknown gar				1												
<i>Lepisosteus</i>	Shortnose gar																
<i>platostomus</i>																	
<i>Hiodon alosoides</i>	Goldeye																
<i>Alosa</i>	Skipjack herring																
<i>chrysochloris</i>																	
<i>Dorosoma</i>	Gizzard shad																
<i>cepedianum</i>																	
<i>Macrhybopsis</i>	Silver chub																
<i>storeriana</i>																	
<i>Platybio</i>	Flathead chub																
<i>gracilis</i>																	
<i>Cyprinella</i>	Red shiner																
<i>lutrensis</i>																	
<i>Cyprinella</i>	Spotfin shiner																

		RKM segment															
Scientific name	Common name	1331	1291	1284	1279	1276	1273	1268	1257	1250	1242	1239	1234	1230	1225	1221	1215
<i>spiloptera</i>																	
<i>Luxilus cornutus</i>	Common shiner								2					2			
<i>Notemigonus crysoleucas</i>	Golden shiner												2				
<i>Notropis sp.</i>	Unkn shiner												3	1	1		
<i>Notropis atherinoides</i>	Emerald shiner	20	26	1221	98	91	42	24	3	44	13	13	45	57	24	20	63
<i>Notropis bleinnius</i>	River shiner	18			1	4	4		1	1	3			4		2	2
<i>Notropis dorsalis</i>	Bigmouth shiner		3	2				7	2	1	18	149	4		9		
<i>Notropis hudsonius</i>	Spottail shiner		3	2	6	1	4	2			5	8	2	2	12	21	13
<i>Notropis stramineus</i>	Sand shiner		4	48	35	13	64	73	48	56	56	19	199	100	81	46	53
<i>Notropis volucellus</i>	Mimic shiner		2	1	1	1	7		3		3	13	2	1			2
<i>Hybognathus argyritis</i>	Western silvery minnow						1		1								1
<i>Phenacobius mirabilis</i>	Suckermouth minnow			1													
<i>Pimephales promelas</i>	Fathead minnow		2								1						1

		RKM segment															
Scientific name	Common name	1331	1291	1284	1279	1276	1273	1268	1257	1250	1242	1239	1234	1230	1225	1221	1215
<i>Cyprinus carpio</i>	Common carp		4			1			2		1	1	4	2	6		
<i>Hypophthalmichthys molitrix</i>	Silver carp													2			
<i>Catostomidae sp.</i>	Unkn sucker				2				2	23	317		48	6			
<i>Carpoides sp.</i>	Unkn carpsucker						1								4	1	
<i>Carpoides carpio</i>	River carpsucker		1	1	7	1	2	2			2	2	11	3	4	1	28
<i>Carpoides cyprinus</i>	Quillback		1		3		1		4	3			2		2		
<i>Catostomus catostomus</i>	Longnose sucker												1				
<i>Cycleptus elongatus</i>	Blue sucker																
<i>Ictiobus sp.</i>	Unkn buffalo		15			1							22				
<i>Ictiobus bubalus</i>	Smallmouth buffalo							1					1	1			1
<i>Ictiobus cyprinellus</i>	Bigmouth buffalo		2	6	6	325	1	6	1	56	173		1	3	9	156	8
<i>Moxostoma sp.</i>	Unkn redhorse			1				2				3	6		17		
<i>Moxostoma macrolepidotum</i>	Shorthead redhorse		6		1	1	2	2	6	13	1	3	55	5		2	18

		RKM segment															
Scientific name	Common name	1331	1291	1284	1279	1276	1273	1268	1257	1250	1242	1239	1234	1230	1225	1221	1215
<i>Moxostoma duquesnei</i>	Black redhorse												7				
<i>Ictalurus spp.</i>	Unkn Ictalurus				1												
<i>Ictalurus punctatus</i>	Channel catfish	1	8	9	42	2	5	5	10	6	2	2	3	24	7	8	6
<i>Morone sp.</i>	Bass sp.		5		1	1									4		
<i>Morone chrysops</i>	White bass	46	18	36	41	7	4	2	5	1	1		18	1	1	1	1
<i>Lepomis macrochirus</i>	Bluegill		1														
<i>Micropterus dolomieu</i>	Smallmouth bass	2	1			1									1		
<i>Micropterus salmoides</i>	Largemouth bass		18												1	2	
	Unidentified		5														
<i>Micropterus spp.</i>	Micropterus spp.																
<i>Pomoxis annularis</i>	White crappie		30		2			1									
<i>Etheostoma nigrum</i>	Johnny darter		6	7	1	13	1	4	1	1	1	1		1			3
<i>Sander sp.</i>	Unkn Sander	4		4	1												

		RKM segment															
Scientific name	Common name	1331	1291	1284	1279	1276	1273	1268	1257	1250	1242	1239	1234	1230	1225	1221	1215
<i>Sander canadense</i>	Sauger		1	1	8						1					1	2
<i>Sander vitreum</i>	Walleye	4	7	13	7	5	2	40		3	6	24	1		4		1
<i>Aplodinotus grunniens</i>	Freshwater drum	25	1	28	110	2	32	3	46	2		9	13	1	17	8	7
<i>Unknown Narrow Bodied</i>					3	16	1	116 7						1			
<i>Unknown Spiny Dorsal or Large Bodied</i>								252		2							
<i>Unidentified</i>					1			1	4					1	2		5

Table 5. Measures of fish species and relative abundance during fish sampling in areas of shallow water habitat near emergent sandbars of the Missouri River (RKM1213- RKM 1331), 2006 – 2008. Results from least squares means (standard errors) [back transformed means] are presented by emergent sandbar type, with associated F-test and level of significance (*P*).

	Mechanically Created	River Created	$F_{1,16}$	<i>P</i>
Species	3.3 (0.5)	3.4 (0.3)	0.03	0.86
Count of fish *	2.1 (0.3) [7.0]	2.2 (0.2) [8.5]	0.31	0.59
Count of Shiners *	1.5 (0.3) [3.7]	1.7 (0.2) [4.6]	0.32	0.58
Count of Size Class 0-1	0.8 (0.2) [1.2]	0.9 (0.1) [1.6]	0.67	0.43
Count of Size Class 2 *	1.1 (0.2) [1.9]	1.1 (0.1) [1.9]	0	0.95
Count of Size Class 3 *	0.7 (0.2) [1.0]	0.8 (0.1) [1.2]	0.19	0.67
Count of Size Class 4 *	1.2 (0.3) [2.3]	1.4 (0.2) [3.2]	0.59	0.45

* Least square means presented are the means at the average of the included covariate, depth, 0.61m.

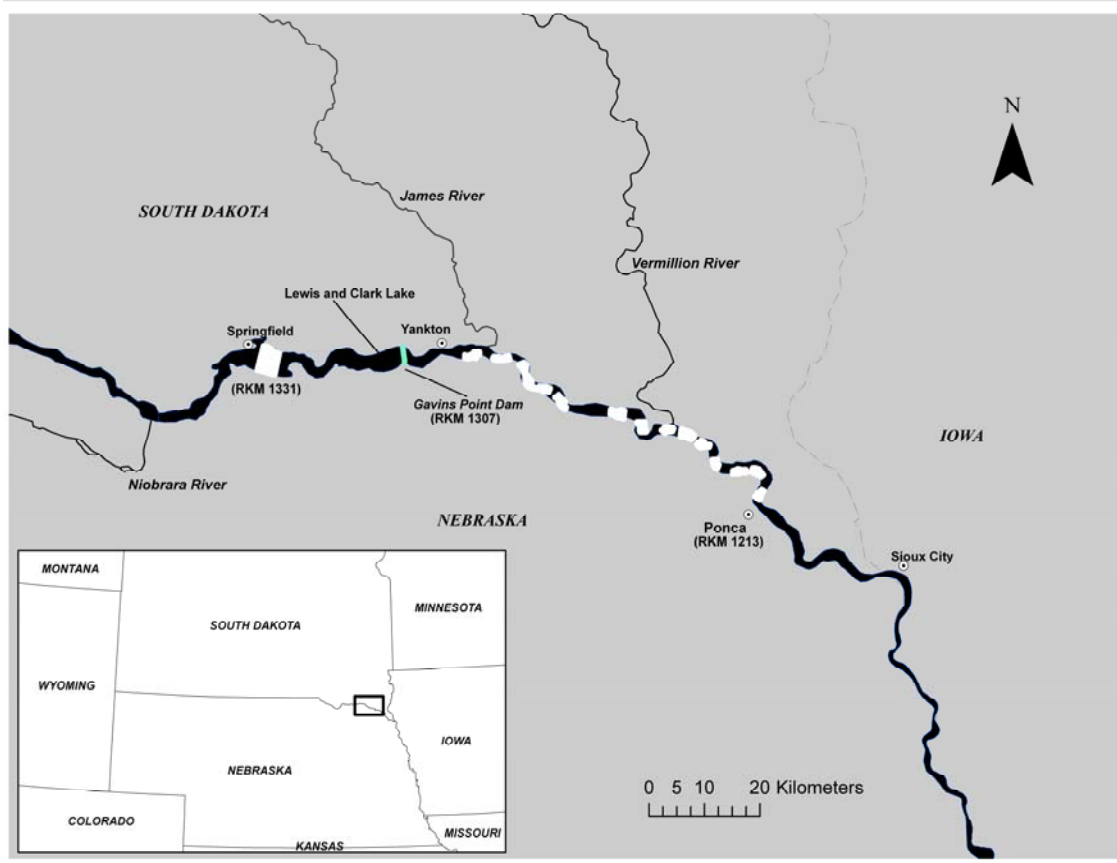


Figure 1. Fish sampling locations (white area) on the Missouri River (black) from 2006-2008, on the Gavins Point Reach (15 sites between Yankton, SD and Ponca, NE) and Lewis & Clark Lake (1 site near Springfield, SD).

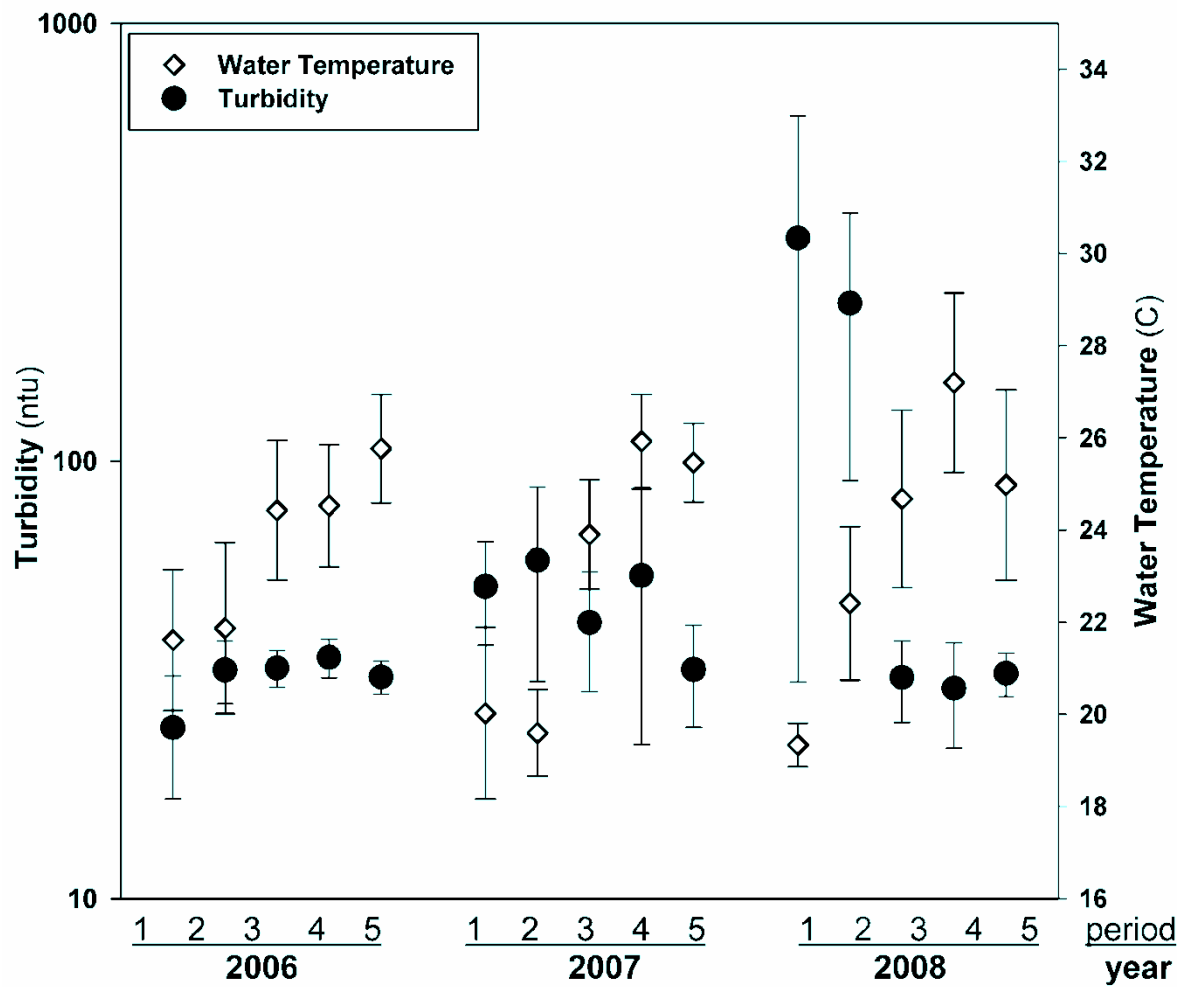


Figure 2. Average water turbidity (ntu) and temperature (°C) with standard deviations during 5 sequential fish sampling periods on Gavins Point Reach and Lewis and Clark Lake during 2006-2008.

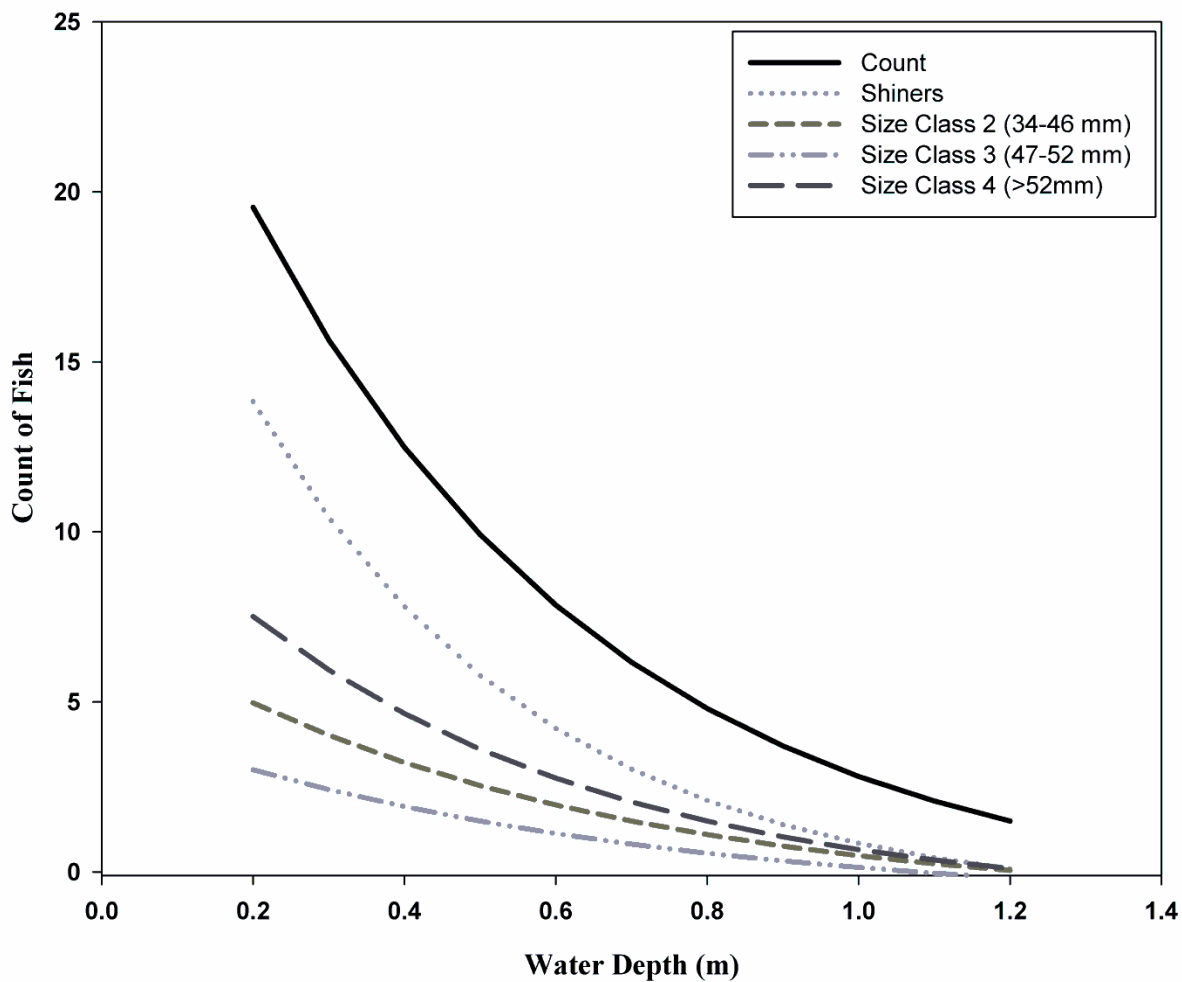


Figure 3. Increasing depths were associated with reduced counts of captured fish. Significant relationships between average water depth of sample sites and measures of fish relative abundance for sampled areas of the Missouri River (RKM1213- RKM 1331) in 2006-2008.

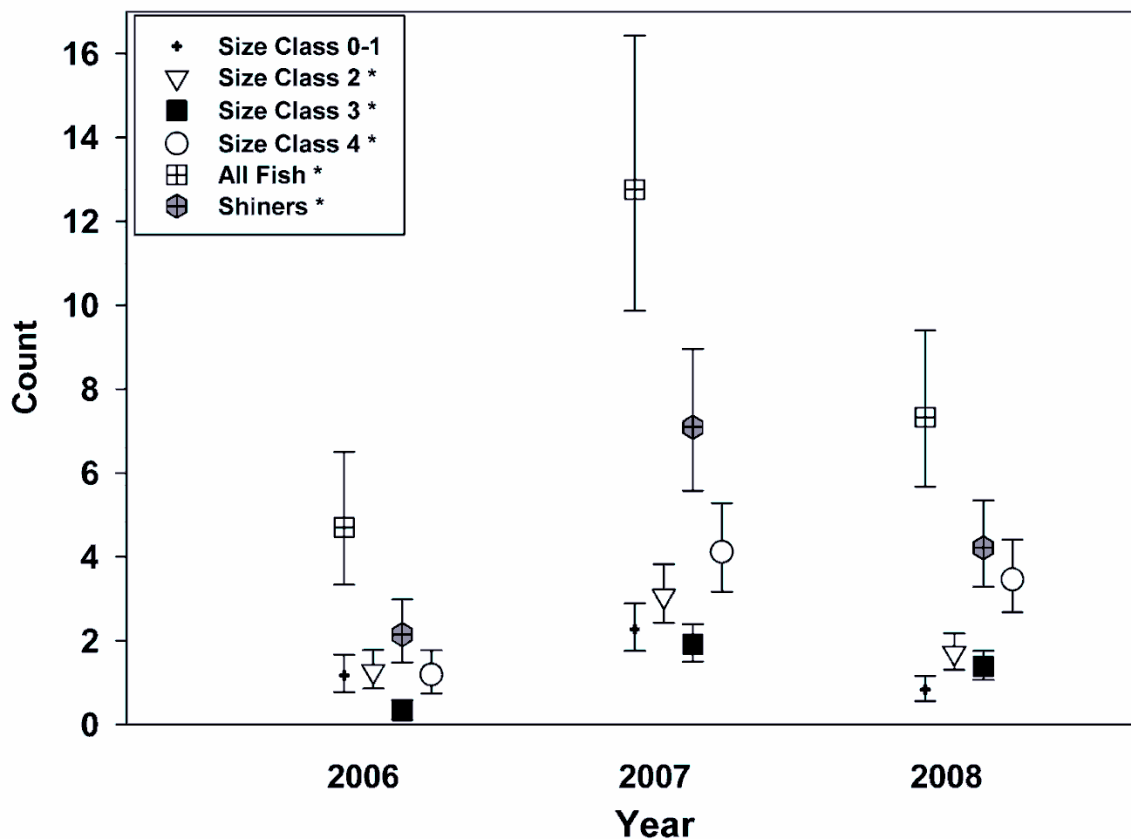


Figure 4. Inter-annual variability in fish relative abundance was observed. Values of fish relative abundance were obtained from back-transformed least squares means and SE within sampled areas of the Missouri River (RKM1213- RKM 1331) in 2006-2008. Significant responses, $P < 0.05$ are indicated by *.

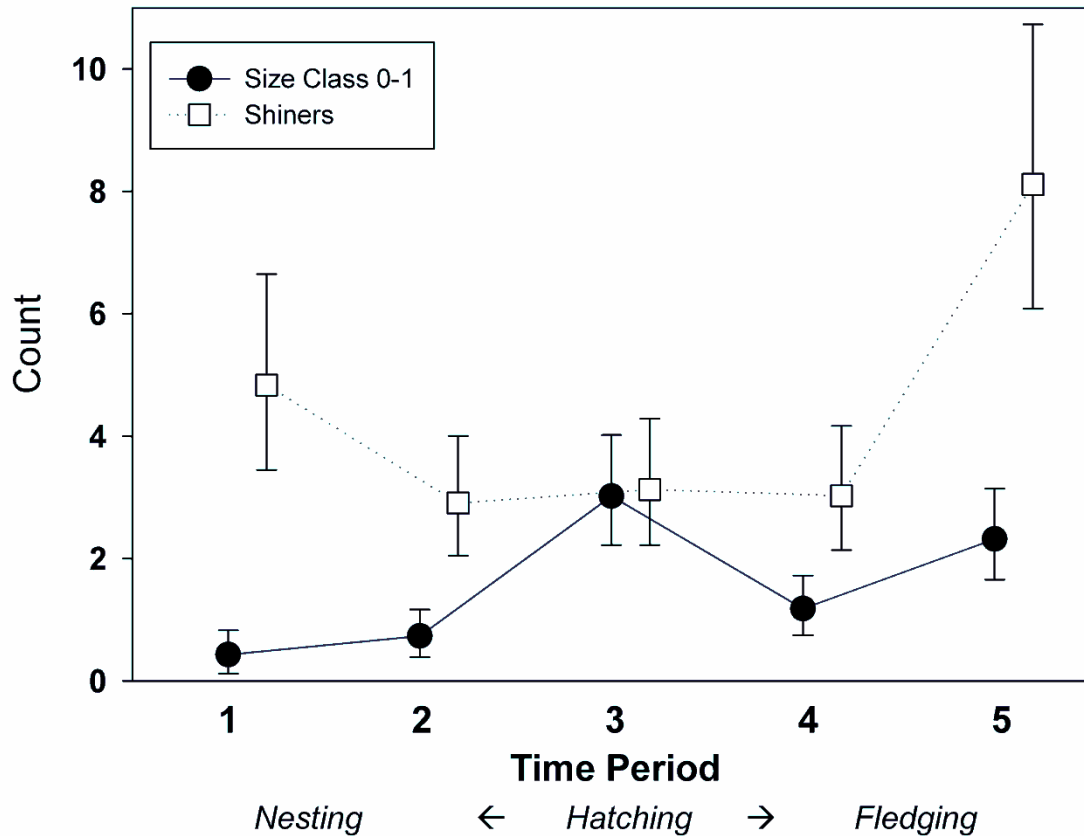


Figure 5. Significant intra-seasonal variability in fish relative abundance was observed for fish size class 0-1 and shiners ($P < 0.05$). Values of fish relative abundance were obtained from back-transformed least squares means and SE within sampled areas of the Missouri River (RKM1213- RKM 1331) in 2006-2008. X-axis indicates time periods sampled and the relationship to Least Tern nesting chronology.

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Chapter 2.

CONSEQUENCES TO LEAST TERN (*STERNULA ANTILLARUM*) OF MICROHABITAT NEST SITE SELECTION ON NATURAL AND MECHANICALLY CONSTRUCTED SANDBARS IN THE MISSOURI RIVER

Interior Least Terns (*Sternula antillarum*) nest on barren sandy habitats, typically sandbars and shorelines within large river systems of the central United States. Loss of natural ecosystem processes that create and maintain these habitats is considered the primary reason for population decline and consequent Federal listing of this population. Throughout their range, management for Least Terns focuses on maintenance of breeding habitats, including placement of dredged material specifically as nesting substrate. Wide expanses of barren land are known to attract Least Terns, yet specific small-scale habitat features are thought to trigger nest habitat selection. This study evaluates nest-scale habitat selection to determine if nest habitats differ between constructed and natural sandbars, and it evaluates the consequences of this selection on nest success. During 2006-2008, 869 Least Tern nest sites on constructed and natural sandbars in the Missouri River were examined for evidence of microhabitat selection at the nest versus habitats within the surrounding area. Significant differences were observed in substrates, amount of debris, and measures of vegetation between natural and created habitats, and between microhabitat at nests and the surrounding area. In general, Least Tern nest sites had coarser and larger substrate materials at the nest, more debris, and shorter and less vegetation compared to areas within the surrounding area. Nests in constructed habitats had a greater proportion of coarse substrates and less vegetation or debris than nests in naturally created habitats. Observed nest success

among constructed sandbars was 1.8x greater than that recorded among nests on natural sandbars, because a greater proportion of nests on natural bars were in or adjoining moist habitats where they were frequently destroyed by inundation. The best-supported model predicting nest success on constructed and natural sandbars each included positive associations with percentage of pebble substrate, but additional habitat predictors differed by sandbar type. Selection of microhabitat characteristics at the nest and vicinity constrains this species to barren water- and wind-scoured habitats. Historically, scoured habitats and the comparative abundance of debris within sites may have been a cue indicating safe habitats as river stage decreased. Water management regimes during this study favored survival of nests on higher-elevation sandbars with limited areas of wet substrates, typically those that were mechanically constructed.

Within the central United States, Least Terns (*Sternula antillarum*) nest on sandbars and shorelines of large rivers. This Interior population is designated as Federally endangered, primarily due to loss of nesting habitats (USFWS 1985). Previous research has examined Least Tern riverine habitat use but preference for specific features used within these habitats remains largely unresolved, in large part due to the visually barren nature of these habitats (Smith and Renken 1991, Kirsch 1996). Within the Missouri River basin, natural hydrological processes that create traditional nesting habitats for Interior Least Terns occur infrequently. Consequently, the U.S. Army Corps of Engineers (USACE) initiated a program to create nesting habitat for Least Terns, and co-occurring Piping Plovers (*Charadrius melodus*), through mechanical placement of dredged materials on the Missouri River (U.S. Fish and Wildlife Service 2003). Use of dredge spoil materials as nesting habitat by Least Terns is well documented throughout North America (e.g. Thompson and Slack 1982, Burger and Gochfeld 1990, Krogh and Schweitzer 1999). From 2004-2008, construction of seven sandbars was completed. During efforts on the Missouri River,

emphasis focused on ensuring the sediment materials used for sandbar substrate materials were sand based (pers.com, Kelly Crane, US Army Corps Engineers), appropriate for nesting Least Terns (Thompson and Slack 1982).

Birds, like Least Terns, provide an opportunity to study habitat selection at micro-scales, as well as the physical processes that create and maintain beach or sandbar habitats for nesting. These habitats are created and maintained by complex high-energy wind and water events, including high flow sediment deposition and transport, wave action, overwash, and scouring by ice and wind. Convergence of these physical processes with succession of vegetation creates a mosaic of microhabitats. Similarly, habitat selection results from a series of behavioral choices at multiple spatial scales resulting in a specific nest site within a home range (Hutto 1985, Block and Brennan 1993, Jones 2001, Mayor et al. 2009). Because selection can occur at multiple spatial scales, understanding scale-specific decision rules that result in fitness consequences is important (Orians and Wittenberger 1991). Therefore, knowledge of microhabitat selection (fourth-order selection; *sensu* Johnson 1980), at the scale of the nest, has great potential for directing subsequent habitat manipulations to enhance use and influence survival. Understanding this human-influenced habitat in the context of geomorphic and ecological processes is also important for identifying the consequences of management actions (Kolbe and Janzen 2002). Among beach-nesting species, the Least Tern nests in habitats described as bare to sparsely vegetated with sand and gravel substrates (reviewed *in* Thompson et al. 1997). As a colonial nesting species, resource defense primarily occurs at the nest (Burger and Gochfeld 1990) and does not appear to include areas at

greater spatial scale (e.g., home range). Consequently, habitat selection within a colony site may have great influence on an individual's fitness through survival of a nest to hatch (hereafter, nest survival).

Studies evaluating Least Tern nesting habitats have been conducted at various spatial scales, with sampling approaches ranging from descriptive analysis to inclusion of systematic and random sampling. At the greatest spatial scale, hundreds of meters, Kirsch (1996) described Least Tern habitats on the Platte River as primarily sand in areas of wider river channel with expansive areas of unvegetated habitats, as well as mid-channel sandbars. In coastal Texas, assessments of colony site selection found that occupied areas were typically larger and of higher elevation, but dominated by sand with <20% vegetation (Thompson and Slack 1982). Based on published data and expert opinion, Carreker (1985) described Least Tern avoidance of silt and use of sand and coarser substrates in a habitat suitability index model. In a small study at a more local scale, Platte River nesting habitats were described (Wilson et al. 1993) as composed of coarse sand and gravel (<6.3 mm diameter) with <10% vegetation cover, and away from areas of dense vegetation or obstructed visibility. At Salt Plains National Wildlife Refuge, Oklahoma, occupied colony areas were >96.7% bare ground, with limited vegetation, driftwood, or debris (Schweitzer and Leslie 1999); substrates were coarser in texture and lighter in color, and located closer to debris and driftwood, than at paired random locations. In coastal areas of New York and New Jersey, nests were observed in stabilized sandy areas with an abundance of small (<1 cm) shell fragments (Burger and Gochfeld 1990), and wide

beaches with a substantial shell component and little vegetation (Gochfeld 1983). Analysis suggested a slightly more complex relationship, with nests closer to vegetation in areas of low vegetation density and farther away in areas of high density (Burger and Gochfeld 1990). While habitat descriptions have been frequent, the importance of habitat features and scale has rarely been related directly to a measure of Least Tern reproduction (although *see* Burger and Gochfeld 1990, Kirsch 1996).

As part of a comprehensive assessment of the response of Interior Least Tern breeding ecology to sandbar habitat creation, we sought to evaluate influences of habitat use on Least Tern nest selection at two different spatial scales. A similar assessment evaluating habitat use within the context of available sandbar habitat found that most features on a sandbar were avoided, but that successful nests were observed in areas with coarser substrates and with less vegetation (density and height) (Sherfy et al. 2012). This study and analysis refines our understanding of available habitat at the time of Least Tern nest selection to be within a 3-m surrounding area as a “context” in which microhabitat selection should have influence on nest survival. Therefore, this study addressed three questions: 1) do microhabitat characteristics at Least Tern nests (1 m² around each nest) and within the surrounding area (3m from each nest) differ between natural river-created and mechanically constructed sandbars? 2) Do habitat features of nest sites differ from those within the surrounding habitat (3m)? 3) Which habitat features are associated with nest success? Results provide greater understanding to guide future habitat management efforts that seek to increase reproductive success of this species within the Missouri River basin.

METHODS

Study Area This study focused on terns nesting within a 135-km segment of the Missouri River between Springfield, South Dakota (42.9°N, 97.8°W) and Ponca, Nebraska USA (42.6°N, 96.7°W). The U.S. Army Corps of Engineers is responsible for primary operational management of the Missouri River, including water control and natural resource management. The area downstream of Gavins Point Dam, the Gavins Point Reach, includes the 59 rivermiles (RM) within the National Park Service's Missouri National Recreational River. Two sampling locations were southeast of Springfield, SD, and within Lewis and Clark Lake, a reservoir on the Missouri River. Within these areas, Least Terns nest on mid-channel sandbars, created through natural river processes (hereafter, *natural* sandbars) or mechanically constructed (hereafter *constructed* sandbars) for Least Terns and Piping Plovers. Constructed sandbars and complexes are created by placing sand-based materials in-channel. In 2006, we identified six sandbar complexes as likely sites for nesting Least Terns, including three natural sandbars/complexes and three constructed complexes. We chose sites based on Least Tern use in previous years (natural sandbars) or after recent creation (constructed sandbars). For each sandbar or complex, we delineated a sampling area 0.5 RM (~0.8 river km) upstream and downstream. We included 1-3 additional sampling sites, natural or created, in each of 2007 and 2008 (Table 1). In 2008, low river levels permitted additional sampling efforts of new low-elevation natural sandbars not available in previous years; new sandbars that were not constructed were categorized as natural sandbars.

Field methods We systematically searched each site for Least Tern nests every 2-3 days from arrival of terns in the study area (mid-May) through the end of nest initiation (early August). We conducted nest habitat assessments at nest discovery, typically during egg laying, prior to onset of incubation. We measured habitat characteristics within a 1-m² square quadrat centered on the nest (hereafter, nest site) and within 4 1-m² square quadrats oriented in cardinal directions 3 m away from the nest (hereafter, surrounding area) (Figure 1). These surrounding area measurements represent both unused habitat, but also a habitat context, or setting, within which nests occur. Habitat features evaluated within each quadrat included substrate moisture (dry or wet), with a detailed classification of the substrate materials, vegetation characteristics, and presence of debris (Table 2). Debris was categorized by size and type: leaf debris, small debris [≤ 2 cm diameter], and large debris [> 2 cm diameter]). Large debris included objects such as bones or logs (Sherfy et al. 2009). In situations where the debris intersected or was within half the diameter of the nest, the site was identified as having “nest furniture” (Figure 2). Surface cover of substrate (%) and vegetation classes were estimated following Daubenmire-type cover class ranges (Sherfy et al. 2008). For each feature we visually assessed categorization based on relative feature cover: 0, >0-5%, 6-15%, 16-30%, 31-45%, 46-70%, and 71-100%. We defined substrate classes based on particle diameter as follows: silt (<0.13 mm), sand (0.13-2 mm), small pebble (2-10 mm), gravel (10-64 mm), and cobble (65-256 mm).

Following discovery, we visited each nest every 2-3 days through incubation to determine nest fate. Use of apparent nest success is appropriate in situations where birds nest on islands, exhibit coloniality, nest loss tends to be catastrophic, and sites are visited frequently (Johnson and Shaffer 1990). We categorized nest fates as successful, unsuccessful, or unknown. A nest was deemed successful if one or more chicks were present in the nest scrape or circumstantial evidence suggested that eggs had hatched (e.g., fragments from hatched egg shells and chick droppings in the scrape; young chicks [<1 day] just outside the nest scrape). An unsuccessful nest fate was assigned if a nest with eggs was destroyed, missing, or could not have hatched based on established incubation stage (e.g., known initiation date and/or egg flotation). An unknown fate was applied sparingly, only if a nest and eggs were missing and there was no evidence of either hatching or loss. We define observed nest success as the percent of successful known fate nests.

Statistics We analyzed habitat data using linear mixed models (SAS – Proc Mixed) to evaluate variation in habitat variables simultaneously between nest sites and surrounding areas (3 m from nest), by sandbar creation method (natural or constructed), and among years. Each habitat variable was treated individually as a response variable. Because many sandbars (14 of 21), were surveyed only a single year, and two other sandbars changed type or were substantially modified between years, we treated each sandbar-by-year combination as a unique sandbar. As each sandbar included multiple nests, each nest was incorporated as a subsample. Consequently in the analysis each subsample (nest and vicinity) was treated as a

subplot within a split-plot design, with each sandbar nested within year and its sandbar creation method. Prior to analyses, we converted the Daubenmire-type cover classes to the midpoints of each class (0, 2.5%, 10%, 23%, 38%, 58%, and 85%). These midpoints were used as a continuous response variable. Similarly, we coded mean and maximum vegetation height midpoints within four heights (m) ranges (0, 0.25(>0 to 0.5), 0.75(>0.5 – 1.0), 1.5 (>1 m)). The 4 surrounding area observations were treated as subsamples, and averaged by nest into a single surrounding area response. To normalize distributions, we transformed counts of cottonwood (*P. deltoids*) stems, willow (*Salix sp.*) stems, and total woody stems using an $\ln(y+1)$ transformation. Following significant main or interaction effects ($\alpha \leq 0.05$), we used Fisher's protected least significant differences to isolate differences between sandbar types, and nest sites from surrounding area. We present least squares means (LSMEAN) and standard errors, or back-transformed means for the three count variables that were log transformed. We assessed nest furniture presence only at nest locations.

We analyzed nest success, the probability of one or more eggs in a nest hatching, to evaluate the consequences of habitat at nest and surrounding area using generalized linear mixed-effects models (lmer, package lme4; Bates, Maechler & Bolker 2011) in R. Based on the results of the habitat analysis, we fit models separately for natural and constructed sandbars to evaluate the influence of habitat on nest fate. We fit models incorporating a binomial distribution and a logit link function with a binary response indicating nest failure or success. Nests were included as

subsamples within each sandbar*year combination to account for potential non-independence. Prior to model development, explanatory variables were screened for correlation with similar habitat variables (e.g. mean and maximum vegetation heights) (Graham 2003). Among parameters with high co-linearity within a given spatial scale (nest or surrounding area), we chose one representative variable which we believed most likely to influence habitat selection. Habitat predictors were included as fixed effects and models constructed using sandbar-by-year combination as random-effects ($n = 18$ and 14 for natural and constructed sandbars, respectively). Substrate moisture was incorporated as a categorical predictor at nest (Sub: wet (0) or dry(1)) and surrounding area (Sur.Sub.wet: all dry (0), ≥ 1 wet (1)). We identified *a priori* candidate models to evaluate influence of habitat features at nest and surrounding based on results from habitat analysis and on personal observation (Table 3). Post-hoc we ran simplified versions of the best fitting model to ensure parsimony or appropriate interpretation of predictor importance. If not among the *a priori* candidate models, the top fitting model for each sandbar type was included post-hoc as a candidate model for the other sandbar type. Using information-theoretic methods we distinguished among competing models using Akaike weights calculated using the small sample-size corrected AIC_c (Burnham and Anderson 2002). Our inference is based on the top fitting models ($\Delta AIC_c \approx 2$), but consideration was given to the importance of inclusion/exclusion of individual parameters when model structure was similar (Anderson and Burnham 2002; Arnold 2010). We report 85% confidence

intervals (CI) as they are more compatible with AIC-based model selection (Arnold 2010).

RESULTS

We documented habitat characteristics and nest fate for 869 Least Tern nests within sampled areas during 2006-2008 (Table 4); 71% were discovered prior to clutch completion. Eighteen percent of nests were located on natural sandbar habitats and 82% on constructed sandbar habitats. We identified several habitat characteristics of nest sites and surrounding areas that differed between natural and constructed sandbar types (Table 5). We detected year effects primarily among vegetation and debris variables. When significant year effects were detected, such that the direction of relationship changed among sandbar types or point types (nest site and surrounding area), we provide details below.

We found 866 of 869 nests on barren sandy substrates (86% dry sand, 14% wet sand) that were largely devoid of vegetation. Among these nests, the annual percentage on dry or wet sand substrates did not differ between natural and constructed habitats, except in 2008 ($\chi^2 = 46.3$, $df = 2$, $P < 0.001$) when 46% of nests in natural habitats and 7% of nests in constructed habitats were located on wet sand. We observed proportionally more nests among wet substrates on natural sandbars (24-51% wet sand) compared to constructed sandbars (7-17% wet substrate) in each year (2006: $\chi^2 = 6.7$, $df = 2$, $P = 0.01$; 2007: $\chi^2 = 9.1$, $df = 2$, $P = 0.03$; 2008: $\chi^2 = 46.3$, $df = 2$, $P < 0.01$).

Substrate Composition

Composition of substrate materials differed between sandbar types (Figure 3), although nest site composition was largely in proportion to composition of the surrounding area, although nests tended to be in areas with coarser substrates than those of the surrounding area. Sand was the predominant substrate material observed at all sites, yet the percentage of sand cover differed among nest, surrounding area, and sandbar type combinations (Table 5). At natural sandbars, nest sites had a greater percentage of sand compared to surrounding areas, whereas percentage of sand on constructed sandbars was similar between nest sites and surrounding areas. Silt, pebble, and gravel differed among nest sites, surrounding areas, and point and sandbar type combinations. Surrounding areas contained more silt than found at nest sites ($P < 0.001$), particularly on natural sandbars ($P < 0.001$), but we did not detect a difference on created sites ($P = 0.097$) where the percentage of silt cover values were consistently low. Nest sites had a greater percentage of pebble and gravel cover than the surrounding area on created sandbars (pebble: $P < 0.01$; gravel: $P < 0.01$), but not on natural sandbars (pebble: $P = 0.39$; gravel: $P = 0.70$). The percentages of cover that were silt and sand differed among site and year combinations (Table 6), with surrounding area having a greater percentage of silt cover than nest sites in 2007 and 2008 but not in 2006; sand was significantly greater among nest sites than the surrounding area in 2008 ($P = 0.001$). Although overall observations of the larger sized materials were small (~2% of area), percentage of gravel and cobble cover was greater for sites on created sandbars than those on natural sandbars. No cobble was observed at nest sites or surrounding areas on natural sandbars. Among the

constructed sandbars, nest sites had a greater percentage of cobble cover than the surrounding area.

Presence of Debris

Measures of debris varied. We did not detect differences between nests on natural and created sandbars for percentage of leaf debris or percentage of small debris. However, we found a greater percent of small debris at nest sites than within surrounding 3 m areas. Percent of small debris varied annually, but in all years we observed more small debris at nest sites than in the surrounding area; the difference was significant only in 2007 ($P < 0.01$). Similarly, nest sites had a greater percentage of large debris cover than the surrounding area, with 78% of surrounding area having no debris. We did not detect differences in the percent of large debris between sandbar types, but the odds of finding debris identified as nest furniture at nests on natural sandbars were twice that of nests on created sandbars. Overall, 56% of all nest sites exhibited nest furniture, but the percentage of occurrence was greater on natural sandbars (70%) than on created sandbars (53%) ($F_{1,26} = 4.86$, $P = 0.04$).

Vegetation

Within the sampled areas, vegetation was limited or absent, averaging ~3% cover with < 1.6 woody stems/m², and vegetation height < 0.25 m. Yet vegetation measures demonstrated significant differences between natural and created habitats, nest and surrounding areas, and years (Table 6-7). Percent woody vegetation cover differed among sandbar types, but level of difference varied among years with some detected among nest/surrounding area and year combinations. Natural sandbars had a

greater percentage of woody vegetation than created sandbars in 2006 ($P < 0.01$), but not in 2007 or 2008. Similarly, nests had a lower percentage of woody vegetation than the surrounding areas in 2006 ($P = 0.054$), but we did not observe differences in 2007 or 2008. Created habitats had less terrestrial vegetation than natural sites.

Percent wetland vegetation did not differ between sandbar types and survey points, but show evidence of differences by year and between constructed and natural sites.

Vegetation heights, both mean and maximum, differed among sandbar type and nest site - surrounding area combinations. Mean vegetation height was greater in the surrounding areas than at nest sites for those on natural sandbars ($P < 0.01$) but not for nests on created sandbars; it was also greater on natural sites than on created sites for both nest sites ($P < 0.02$) and surrounding areas ($P < 0.001$). The relationship was similar for maximum vegetation height, with those in surrounding areas higher than at the nests on natural sandbars ($P < 0.02$) but not for those on created sandbars; it was also greater on natural sites than created sites for both nest sites ($P < 0.01$) and surrounding areas ($P < 0.001$).

Differences in vegetation were also observed among the counts of woody stems, which differed between natural and created sandbars, survey areas, and years. Nests on natural sandbars had more woody stems than those on created sandbars ($P < 0.05$). Overall, nest sites had fewer total woody stems than surrounding areas ($P < 0.01$) but significance depended somewhat on year; we detected differences in 2006 ($P = 0.04$) and 2007 ($P < 0.001$) but not in 2008. Among woody stems, cottonwood stem counts differed between natural and created sandbars, nest sites and surrounding

areas, and year. Counts of cottonwood stems were greatest in 2006 (1.2 stems/m²) and differed from those observed in 2007 or 2008 (0.3 stems/m²). We detected differences overall in the count of cottonwood stems with greater abundance on natural sandbars than created sandbars and at 3-m surrounding areas than at nest sites. Among willow stem counts, we detected differences among nest site - surrounding area combinations and among nest site - surrounding area and year combinations. Counts of willow stems were greatest in 2006 (0.6 stems/m²), and differed from those observed in 2008 (0.1 stems/m²) ($P=0.03$), but not 2007 (0.4 stems/m²; $P<0.4$). Cottonwood stem abundance was greater at 3-m surrounding areas than at nest sites on natural ($P<0.001$) and constructed sites ($P=0.001$); natural and created sites did not differ at surrounding areas ($P=0.12$) or nest sites ($P=0.39$).

Influence of Habitat Features on Nest Fate

We determined fate, success or failure, for 95% of nests. Nest success among constructed sandbars (70%, $n = 675$) was greater than that observed among nests on natural sandbars (37%, $n=149$). Our best-supported models of nest fate on natural (Table 8) and constructed sandbars (Table 9) included positive associations with pebble substrate materials (Fig. 4) but varied by sandbar type on the inclusion of additional predictors describing substrate, vegetation, debris or substrate moisture. Subtle differences in the key physical habitat predictors were observed among sandbar types, but also by nest fate (Table 8.)

Our model for nest success among natural sandbars was well supported, based on 85% CI, for each of the six included predictor variables. Nest failure was ~25%

more likely in the presence of any wet substrate in the surrounding area ($\beta_{Sur.SubWet}$ CI = -2.0 to -0.1). Similarly, terrestrial vegetation (β_{TerVeg} CI = -0.5 to -0.02) was negatively associated with nest success. Positive predictors of nest success include the percent of pebble at the nest (β_{Pebble} CI = 0.002 to 0.04) and the percentage of large debris in the surrounding area ($\beta_{Sur.DebrisLrg}$ CI = 0.18 to 0.65). Two measures of vegetation, maximum vegetation height (β_{MaxHt} CI = 1.65 to 5.58) and woody stem count ($\beta_{\log_n(Stems + 1)}$ CI = 0.16 to 1.02) (Fig. 5) were also associated with nest success. Thus, where π is the predicted probability of nest success, our best-supported model among natural sandbar site candidate models is represented as

$$\begin{aligned} \text{logit}(\pi)_{\text{natural sandbars}} = & \\ & -1.67 - 1.05\text{Sur.SubWet} + 0.42\text{Sur.DebrisLrg} + \\ & 0.02\text{Pebble} + 3.61\text{MaxHt} - 0.26\text{TerVeg} + \\ & 0.59 \log_n(\text{Stems} + 1) + \varepsilon_{\text{Sandbar*Year}} \end{aligned}$$

with $\varepsilon_{\text{Sandbar*Year}}$ representing a random effect of Sandbar*Year, with $\hat{\sigma}^2 = 2.05$.

In contrast to natural sandbars, model selection procedures for constructed sandbars (Table 9) indicated that the best fitting candidate model included five covariate predictors, of which three were well supported, based on 85% CI. Nest failure predictions increased with the abundance of woody stems in the surrounding area ($\beta_{\log_n(Sur.Stems + 1)}$ CI = -0.44 to -0.02) (Fig 5). Nest success was positively associated with percent of pebble (β_{Pebble} CI = 0.004 to 0.03) and cobble substrates (β_{Cobble} CI = 0.05 to 0.41) at the nest; inclusion of gravel in the model did not improve model fit

(Model: Combination - (TerVeg -Stems) $\Delta AIC_c = 1.95$ from best-supported model). Although retention of two variables, maximum vegetation height and surrounding area vegetation height, improved model fit, their inclusion was not strongly supported (β_{MaxHt} CI = -1.57 to 1.38; $\beta_{Sur.MaxHt}$ CI = -0.95 to 1.03) and the model may be overfitting; consequently the importance of these measures of vegetation height for influencing nest fate remains unclear. Thus, among the constructed sandbar sites, the model with the best support is represented as

$$\begin{aligned} \text{logit}(\pi)_{\text{constructed sandbars}} = & 0.86 + 0.01 \text{Pebble} + 0.23 \text{Cobble} - \\ & 0.10 \text{MaxHt} + 0.04 \text{Sur.MaxHt} - 0.23 \log_n(\text{Sur.Stems} + 1) + \\ & \varepsilon_{\text{Sandbar*Year}} \end{aligned}$$

with $\varepsilon_{\text{Sandbar*Year}}$ representing a random effect of Sandbar*Year, with $\hat{\sigma}^2 = 0.60$.

DISCUSSION

Although the breeding range of Least Terns within North America is relatively broad, natural sandy barren habitats are limited, and management efforts have frequently focused on the creation or maintenance of suitable nesting habitat (Thompson and Slack 1982; Krogh and Schweitzer 1999; Erwin and Beck 2007; Spear *et al.* 2007; Sherfy *et al.* 2012). With multiple spatial scales of physical processes determining habitat conditions for nesting, it is notable that microhabitat selection, as documented by this study, may further constrain occupation of apparently available habitats during breeding. Furthermore, the nest location decision influences nest fate. Least Terns occupy habitats subject to direct physical processes of wind and water action on substrate, vegetation, and debris. Constructed habitats,

in 1-3 years following creation, may not have received the full range of physical weathering and erosion that create conditions preferred by this species. Nevertheless, we document both occupation and nest success within constructed habitats suggesting that many of the habitat requirements are met.

Least Tern nests within sampled areas of the Missouri River were located within habitats largely similar to those described elsewhere (Gochfeld 1983, Thompson and Slack 1983, Burger and Gochfeld 1990, Wilson et al. 1993, Schweitzer and Leslie 1999). However, in contrast to other studies, our sampling effort allowed us to identify the range of nearby conditions encountered at nest initiation and to explore the consequences of habitat features on nest fate. Others have reported Least Terns nest in dry habitats, whereas 14% of nests in this study were first observed in wet substrate habitats. Although Least Terns that initiated nests near wet substrate exhibited reduced rates of apparent nest success, 10% of successful nests were first observed in wet substrate habitats. Burger and Gochfeld (1990) also observed reduced rates of success for nests observed in areas near the water. Researchers and managers seeking to document nesting and nest success need to include moist habitats within their survey areas, recognizing that differences may exist in observed nest success.

Among both sandbar types, Least Tern apparent preference for nest initiation with areas of coarse substrates agrees with studies elsewhere (Burger and Gochfeld 1999; Schweitzer and Leslie 1999; Sherfy *et al.* 2012). Although pebble abundance was not identified as a key feature for nest habitat selection, except on constructed

sandbars, it was a positive predictor of nest success at both sandbar types. In contrast, we previously identified pebble as a feature selected against on constructed sandbars, with little documented difference on nest success (Sherfy *et al.* 2012). Among the constructed sandbars, nests were in areas with more cobble, gravel, and pebbles, than surrounding areas. Similarly, on natural sandbars Least Tern nests were in areas with more sand and less silt than surrounding areas. Subtle substrate difference between the nest and the surrounding area were frequently context-specific, by habitat type or year, but there was consistent avoidance of the finest substrates material (e.g. silt). In Texas, Thompson and Slack (1982) suggested limiting the proportion of silt and clay in dredged materials intended for nesting colonies; silt and clay adhere to eggs, reducing egg shell respiration, and can inhibit turning. Differences in substrate selection in these habitats likely reflect variation in the physical processes at work, particularly inundation of natural habitats, as compared to aeolian processes in the higher-elevation constructed habitats.

The apparent attraction of Least Terns to debris is clear, yet the adaptive significance of this behavior is unknown. Debris may provide camouflage for nests and/or incubating adults, visual separation from neighboring nests, and it may modify nest microclimate, particularly temperature and humidity. When large and small debris items were present, they tended to be more abundant at the nest than in the surrounding area, depending in part on annual debris abundance. Other investigators have also noted the close proximity of Least Tern nests to debris (Grover and Knopf 1982; Smith and Renken 1991; Schweitzer and Leslie 1999; Sherfy *et al.* 2012).

Large debris in the surrounding area was included in our best supported models of nest success among natural sandbars, although other measures of debris at nest site and nest furniture were not.

Vegetation abundance and height in our study also tended to be lowest at the nest sites and higher in surrounding areas. But we also documented a positive effect of woody stems on nest survival among natural sandbars, a result also observed at a larger spatial scale (Sherfy *et al.* 2012). Yet among constructed sandbars, nest success declined with increases in mean stem counts within the surrounding area. Vegetation avoidance was noted by others (Burger and Gochfeld 1990; Gochfeld 1983; Kirsch 1996; Schweitzer and Leslie 1999; Thompson and Slack 1982; Wilson *et al.* 1993), although attraction to sparse vegetation has also been observed (Burger and Gochfeld, 1990). While limited densities of woody vegetation appear acceptable, Least Tern nest success is negatively associated with abundance of terrestrial vegetation, (e.g. forbs). Although we found statistical differences between nests located on created and natural sandbars, there are also biological consequences of habitat selection on nest fate among constructed and natural sandbars. Natural sandbars tended to demonstrate characteristics consistent with more exposure to river inundation (more wet substrate habitat, slightly more silt in proximity to nests), but also areas displaying evidence of wind action (less sand and more pebble) within drier areas. Vegetation establishment and succession on sandbars influences the extent and availability of suitable nesting habitat for Least Terns on the Missouri River, as it does elsewhere in the Great Plains (Leslie *et al.* 2000; Sherfy *et al.* 2012;

Sidle et al. 1992). Surrounding nest areas on natural sandbars have established vegetation, with greater percentage of vegetation (woody and terrestrial), greater vegetation heights (mean and maximum), and greater stem densities (cottonwood and woody vegetation stems) than nests on constructed habitats. Thompson and Slack (1982) noted that colonies on natural areas tended to be composed of fewer nests and were at a lower elevation, relative to mean low water and high tide, than colonies on dredge spoil material. Although elevation was not measured in this study, results presented here, and field observations (JHS) are consistent with currently available natural sandbars characterized by a lower elevation profile, less vertical relief and smaller size; areas of higher relief, not subject to overwash and erosion, and frequently vegetated. Presence of wet substrate within 3 m of nests on these sandbars was a significant predictor of nest failure. Visher (1915) noted that colonies near the Vermilion River (i.e. sandbars of Missouri River at Vermilion River confluence) were small with “not more than seven or eight pairs.” This description is consistent with sizes of colonies on low elevation natural sandbar habitats observed during this study. Subsequent to this study, high elevation sandbars were deposited throughout the study area by record flooding in 2011.

The function of large and small debris near Least Tern nests is unclear. What is evident is that nests in natural habitats have twice the odds of being placed next to debris than do those on constructed sandbars. High association of nests in natural habitats with debris suggests a possible adaptive benefit to nest survival with presence of debris. However, nest success did not increase among nests with debris, only those

in proximity to debris at the nest or within the surrounding area. Compared to Mayfield nest success rates reported by Smith and Renken (1993) (survival to 21-days 51-68%), nest success on Missouri River constructed sandbars is similar, but reduced among the lower elevation natural sandbars. Historically, Interior Least Terns nested on sandbars of large rivers as the peak flows receded in summer (Ganier 1930), and as these flows receded, debris was retained on the sandbars (Smith and Renken 1991). On these newly scoured habitats, frequently damp, it was advantageous to nest quickly, maximizing the opportunity to reproduce. Currently, flows in this area of the Missouri River are fluctuated regularly during river operations, with generally increasing discharge during the nesting season (Fig. 5), such that areas with damp substrates, particularly low elevation sandbars, will later be inundated rather than result in high and dry safe nesting habitats. Throughout coastal areas, birds frequently nest in or just above the wrack and debris lines, a level that is generally safe from waves and most tidal action (Lauro and Burger 1989). A similar pattern was also observed on sandbars of the Mississippi River (Smith and Renken 1991). In the Salt Plains of Oklahoma where debris distribution was relatively even, Least Terns nested by debris but also closer to the water than would be expected (Grover and Knopf 1982). Within our study area, it is likely that the wet substrate and wrack line, which historically signaled low-risk emerging habitats, are not safe from flooding under current river management, a finding noted previously by Schwalbach *et al.*, (1993). While management of debris is possible, the affinity of

terns for nesting near water suggests that management of nest debris may also require consideration of distance to water, and annual water management plans.

While habitat selection is based on specific features, such as a nest cavity or appropriate substrates, yet it is the formative processes create combinations of features present, the niche gestalt (James 1971, James et al.2001). Least Terns appear to exhibit microhabitat selection in nest placement, and the microhabitat selection differs between habitat creation types, likely a consequence of the processes to which the habitats are exposed. Overall, the Least Tern niche gestalt for nest site selection appears to minimize the coverage of silt and vegetation, while maximizing percentages of coarser substrate materials (e. g. pebbles, gravel, cobble), and debris (small and large). We observed increases in nest success in association with pebble substrates, and other features indicative of a relatively “stable” habitat. Within the narrow conditions of sampled areas, upper threshold limits in selection for these characteristics at the nest, particularly pebble, gravel and debris, cannot be established, but could be manipulated through management to determine optimal conditions for selection and nest success. While nest success is the first step in achieving reproductive success, further analysis will evaluate if nest success, and daily nest survival, are correlated with increased reproductive success.

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Table 1. Study site sampling locations for nesting habitat, river mile boundaries, and sandbar types within those boundaries for 2006 – 2008. Sandbar types are indicated by their creation type, N (natural) and C (constructed); both letters indicate different sandbars within sites.

Site	River miles		River kilometers		
	Downstream -	Downstream -	2006	2007	2008
	Upstream	Upstream			
755	754.3 - 755.4	1213.9 - 1215.6	C	C	C
759	758.2 - 759.7	1220.2 - 1222.6			N
761	760.5 - 762.1	1223.9 - 1226.4	C	C	N C
770	769.1 - 770.8	1237.7 - 1240.4	C	C	N C
775	774.4 - 775.6	1246.2 - 1248.2			C
776	775.6 - 776.8	1248.2 - 1250.1			N
777	776.8 - 778.1	1250.1 - 1252.2			C
779	778.4 - 779.4	1252.7 - 1254.3			N
781	780.6 - 782.2	1256.2 - 1258.8	N		
783	781.8 - 783.1	1258.1 - 1260.2		N	N
791	790.8 - 792.1	1272.6 - 1274.7	N	N	C

795	794.6 - 795.9	1278.7 - 1280.8	N	N	N
796	795.9 - 797.7	1280.8 - 1283.8		N	N
802	801.5 - 803.4	1289.9 - 1292.9			N
827	825.6 - 827.6	1328.6 - 1331.8		C	C
835	833.6 - 834.8	1341.5 - 1343.5		N	

Table 2. Habitat variables quantified and used to evaluate nest success at least tern nest sites and surrounding area on constructed and natural sandbars on the Missouri River, 2006-2008.

Variable	Habitat Area Assessed	Nest Success Predictors	
		nest	Surrounding Area (Sur.)
<i><u>Substrate</u></i>			
%Cobble	Nest, Surrounding Area	Cobble	Sur.Cobble
%Gravel	Nest, Surrounding Area	Gravel	Sur. Gravel
%Pebble	Nest, Surrounding Area	Pebble	Sur.Pebble
%Sand	Nest, Surrounding Area	Sand	Sur.Sand
%Silt	Nest, Surrounding Area	Silt	Sur.Silt
Substrate Moisture	Nest, Surrounding Area	Sub	Sur.Subwet
<i><u>Debris</u></i>			
Nest Furniture	Nest	NestFurn	
%Large Debris	Nest, Surrounding Area	DebrisLrg	Sur.DebrisLrg
%Small debris	Nest, Surrounding Area	DebrisSml	Sur.DebrisSml
%Leaf litter	Nest, Surrounding Area		
<i><u>Vegetation</u></i>			
Max Height(m)	Nest, Surrounding Area	MaxHt	Sur.MaxHt
Mean Height (m)	Nest, Surrounding Area		
%Terrestrial	Nest, Surrounding Area	TerVeg	Sur.TerVeg
%Woody	Nest, Surrounding Area		
%Wetland	Nest, Surrounding Area		

Stem counts

Woody	Nest, Surrounding Area	Stems	Sur.Stem
Cottonwood	Nest, Surrounding Area		
Willow	Nest, Surrounding Area		

Table 3. Nest success models identified a priori for evaluation on mechanically created and natural sandbars.

Model Name	Nest Success Predictors
Nest-and-Area	Gravel + Sur.Gravel + MaxHt+ Sur.MaxVegHt
Sandbar ^a	Gravel + Cobble + MaxHt+ TerVeg+ Stems
Sandbar-II	Sur.Sub.wet + Sur.DebrisLrg + Pebble + MaxHt+ TerVeg+ Stems
Nest	Sand*Sur.Sand + Silt*Sur.Silt + DebrisLrg*Sur.DebrisLrg + DebrisSml*Sur.DebrisSml + MaxVegHt*Sur.MaxHt+ TerrestrialVeg*Sur.TerVeg+ Stems*Sur.Stems
Debris & Moisture	Sub + NestFurn+ Sur.Sub.wet + DebrisLrg*Sur.DebrisLrg
Debris & Moisture Plus	NestFurn + Sub + Sur.Sub.wet + Pebble*Sur.Pebble + Silt*Sur.Silt + Gravel*Sur.Gravel + DebrisLrg*Sur.DebrisLrg
Natural_Habitat	Silt + Sand + DebrisLrg + MaxHt

Natural_Habitat.surrounding	Sur.Silt + Sur.Sand + Sur.DebrisLrg + Sur.MaxHt
Natural_Habitat.interaction + Debris & Moisture	Sub + Sur.Sub.wet + NestFurn+ MaxVegHt*Sur.MaxHt+ Silt*Sur.Silt + Sand*Sur.Sand + DebrisSml*Sur.DebrisSml + DebrisLrg*Sur.DebrisLrg
Natural_Habitat.interaction	Silt*Sur.Silt + Sand*Sur.Sand + MaxVegHt*Sur.MaxHt + DebrisLrg*Sur.DebrisLrg
Mechanical_Habitat ^a	Stems + Pebble + Gravel + Cobble + DebrisSml
Mechanical_Habitat.surrounding ^a	Sur.Stems + Sur.Pebble + Sur.Gravel + Sur.Cobble + Sur.DebrisLrg
Mechanical_Habitat.interaction ^a	Stems*Sur.Stems + Pebble*Sur.Pebble + Gravel*Sur.Gravel + Cobble*Sur.Cobble + DebrisLrg*Sur.DebrisLrg
Combination ^a	Gravel + Pebble + Cobble + MaxHt+ Sur.MaxHt+ TerVeg+ Stems + Sur.Stems
Combination.interaction ^a	Gravel + Pebble + Cobble + MaxVegHt*Sur.MaxHt+ TerVeg+ Stems*Sur.Stems
Combination Plus ^a	NestFurn+ Sub + Sur.Sub.wet + Gravel + Pebble + Cobble + MaxHt+ Sur.MaxHt+ TerVeg+ Stems + Sur.Stems

^a Predictor *Cobble* included in models on constructed sandbar.

Table 4. Count of Least Tern nests and surrounding area habitat assessments included in study by point type (nest, surrounding area) on natural and constructed sandbars, for year of the study.

Year	Natural		Constructed		Nest Total
	Nest	Surrounding Area	Nest	Surrounding Area	
2006	64	64	208	208	272
2007	52	52	212	212	264
2008	40	40	293	286	333
Total	156	156	713	706	869

Table 5. Least Tern nest and nest areas habitat characteristics on sampled sandbars within the Missouri River (Gavins Point Reach, and Lewis and Clark Lake), 2006 – 2008. Results from least squares means (standard errors) [back transformed means] are presented by sandbar type (mechanically created and natural) by survey point (nest and 3m area). Significant pair wise differences ($P < 0.05$) are indicated if significant sandbar type * point interactions were noted: X (between nest and 3m-area within a sandbar type, $F_{1, 26}$), N (nests between sandbar types), A (3m-surrounding area between sandbar types). Significant main effects are reported, and indicated by S (sandbar type; $F_{1, 26}$) or P (between nests and 3m; $F_{1, 26}$), and Y (year; $F_{2, 26}$).

<u>Substrate</u>	<u>Sandbar Type</u>	<u>Survey Point</u>		<u>Main Effects</u>	<u>Sandbar Type * Interaction</u>	
		<u>Nest</u>	<u>3m Area</u>		<u>Survey Point</u>	<u>Contrasts</u>
%Cobble	Constructed	0.31 (0.06)	X	S: 6.01, $P = 0.02$	2.32, $P = 0.14$	
	Natural	0 (0.09)	0 (0.09)			
%Gravel	Constructed	1.99 (0.17)	X	S: 25.96, $P < 0.001$	4.62, $P = 0.04$	N A
	Natural	0.31 (0.25)	0.40 (0.25)			
%Pebble	Constructed	13.56 (4.69)	X		6.34, $P = 0.02$	
	Natural	17.42 (4.25)	18.01(4.25)			
%Sand	Constructed	72.74 (4.04)	72.66 (4.04)	P: 8.42, $P = 0.008$	7.65, $P = 0.01$	

	<u>Sandbar Type</u>	<u>Survey Point</u>	<u>Main Effects</u>	<u>Sandbar Type *</u>	<u>Interaction</u>
%Silt	Natural	69.81 (3.85) X	66.40 (3.85)		
	Constructed	3.53(2.46)	4.43 (2.46)	P: 18.31, $P <$	
	Natural	4.96 (2.47) X	8.27 (2.47)	0.001	6.01, $P = 0.02$
<u>Debris</u>					
%Large Debris	Constructed	2.47 (0.36) X	0.82 (0.36)	P: 41.6, $P < 0.001$	0.47, $P = 0.50$
	Natural	3.16 (0.43) X	1.13 (0.43)		
%Small debris		<u>Nest</u>	<u>3m Area</u>		
	Constructed	2.55 (0.35)	1.44(0.35)	P: 10.13, $P <$	
	Natural	2.73 (0.40)	1.92 (0.40)	0.004	0.26, $P = 0.61$
%Leaf litter	Constructed	0.15 (0.06)	0.11 (0.06)	Y: 7.48, $P < 0.003$	
	Natural	0.05 (0.08)	0.11 (0.08)		1.71, $P = 0.20$
<u>Vegetation</u>					
Max	Constructed	0.08 (0.02)	0.09 (0.02)	S: 13.64, $P =$	4.03, $P = 0.055$
					N A

	<u>Sandbar Type</u>	<u>Survey Point</u>	<u>Main Effects</u>	<u>Sandbar Type *</u>	<u>Interaction</u>
Height(m)			0.001		
	Natural	0.17 (0.02) X	0.21 (0.02) P: 4.33, $P < 0.048$		
Mean	Constructed	0.08 (0.02)	0.08 (0.02) S: 11.91, $P < 0.002$		
Height (m)	Natural	0.15 (0.02) X	0.19 (0.02) P: 5.35, $P = 0.03$	8.79, $P = 0.006$	N A
%Terrestria	Constructed	0.44 (0.27)	0.38 (0.27) S: 13.20, $P = 0.001$	0.931, $P = 0.34$	
I	Natural	1.72 (0.28)	1.82 (0.28)		
%Woody	Constructed	0.51 (0.19)	0.61 (0.19) S: 8.10, $P < 0.009$	0.00, $P = 0.97$	
	Natural	1.25 (0.19)	1.34 (0.19) Y: 5.64, $P = 0.009$		
%Wetland	Constructed	0.25 (0.13)	0.36 (0.13)	0.01, $P = 0.94$	
	Natural	0.40 (0.15)	0.52 (0.15)		
<u>Stem counts</u>					
Woody	Constructed	0.34 (0.15) [0.40]	0.46 (0.15) S: 5.59, $P = 0.03$	6.01, $P = 0.02$	
			[0.58] P: 5.92, $P = 0.02$		

<u>Sandbar Type</u>		<u>Survey Point</u>		<u>Main Effects</u>	<u>Sandbar Type *</u>		<u>Interaction</u>
Natural		0.76 (0.14)	0.95 (0.14)	Y: 3.95, $P = 0.032$			
		[1.14]	[1.59]				
Cottonwood	Constructed	0.2 (0.13)	0.29 (0.13)	S: 5.12, $P = 0.03$			
		[0.22]	[0.34]	P: 16.42, $P <$		0.0.74, $P = 0.40$	
Natural		0.61 (0.12)	0.69 (0.12)	0.001			
		[0.84]	[0.99]	Y: 3.43, $P = 0.048$			
Willow	Constructed	0.19 (0.09)	0.27 (0.09)				
		[0.21]	[0.31]	P: 31.55, $P <$		3.79, $P = 0.06$	
Natural		0.29 (0.08)	0.46 (0.08)	0.001			
		[0.34]	[0.58]				

Table 6. Significant and marginally significant point by year interaction. Least squares means (standard errors) [back-transformed means] are given for each point and year combination (back-transformed means given only where relevant). Different letters within a row indicate significant differences within that row at the $\alpha=0.05$ significance level. An asterisk next to a column header indicates significant differences, at the 0.05 level, between the two rows below that header.

		2006	2007 *	2008 *
Silt	$F_{2,26} = 5.90$, Nest	0.55 (3.40) a	6.65 (3.04) a	5.55 (2.55) a
	$P = 0.008$, Surrounding Area	0.52 (3.40) a	8.86 (3.04) ab	9.68 (2.55) b
		2006	2007	2008 *
Sand	$F_{2,26} = 4.40$, Nest	78.48 (5.52) a	66.84 (4.90) a	68.51 (3.96) a
	$P = 0.01$, Surrounding Area	78.80 (5.52) a	65.34 (4.90) ab	64.44 (3.96) b
		2006	2007	2008
%Woody	$F_{2,26} = 2.69$, Nest	1.43 (0.26) a	0.60 (0.23) b	0.61 (0.20) b
	$P = 0.09$, Surrounding Area	1.69 (0.26) a	0.78 (0.23) b	0.46 (0.20) b
		2006 *	2007 *	2008
Willow	$F_{2,26} = 7.11$, Nest	0.35 (0.12) [0.42] a	0.25 (0.10) [0.28] a	0.13 (0.09) [0.14] a
	$P = 0.003$, Area	0.56 (0.12) [0.75] a	0.40 (0.10) [0.49] ab	0.14 (0.09) [0.15] b
Woody	$F_{2,26} = 3.40$,	2006 *	2007 *	2008

$P = 0.05$	Nest	0.93 (0.20) [1.53] a	0.38 (0.18) [0.46] b	0.34 (0.15) [0.41] b	
	Area	1.08 (0.20) [1.93] a	0.65 (0.18) [0.92] ab	0.38 (0.15) [0.46] b	

Table 7. Significant sandbar type by year interactions. Least squares means (standard errors) [back-transformed means] are given for each sandbar type and year combination (back-transformed means only given where relevant). Different letters within a row indicate significant differences within that row at the $P = 0.05$ significance level. An asterisk next to a column header indicates significant differences, at the $P = 0.05$ level, between the two rows below that header.

		2006		2007		2008*	
%Wetland	$F_{2,26} = 3.99,$	Constructed	0.15 (0.26) a	0.61 (0.22) a	0.16 (0.17) a		
	$P = 0.03$	Natural	0.48 (0.26) ab	0.07 (0.24) b	0.85 (0.24) a		
		2006 *		2007		2008	
%Woody	$F_{2,26} = 4.14,$	Constructed	0.69 (0.37) a	0.68 (0.32) a	0.37 (0.25) a		
	$P = 0.03$	Natural	2.48 (0.34) a	0.70 (0.31) b	0.70 (0.28) b		

Table 8. Logistic regression models and model selection results for evaluating the relationship of nest habitat on Least Tern nest fate on natural sandbars of the Missouri River, 2006-2008.

Model Name	K ^a	ΔAIC_c^b	ω_i^c
Sandbar-II	8	0.00	0.85
Sandbar-II - TerVeg ^e	7	3.65	0.14
Sandbar	6	10.21	0.01
Natural_Habitat + Sandbar	8	10.60	0.00
Natural_Habitat	6	12.91	0.00
Combination	9	13.76	0.00
Combination - (TerVeg -Stems) ^f	7	14.85	0.00
Combination + (Sub + Sur.Sub.wet + NestFurn)	12	14.96	0.00
Nest-and-Area	6	15.61	0.00
Mechanical_Habitat.surrounding	6	16.81	0.00
Combination.interaction	11	17.88	0.00
Natural_Habitat.surrounding	6	19.31	0.00
Mechanical_Habitat	6	20.51	0.00
Debris & Moisture	8	20.60	0.00
Nest	23	25.20	0.00
Mechanical_Habitat.int	14	27.72	0.00
Debris, Moisture, Coarse Substrate & Nest Furniture	15	32.02	0.00
Natural_Habitat.interaction + Debris & Moisture	20	33.38	0.00
Natural_Habitat.interaction	12	33.86	0.00

^a Number of predictors in the model, includes terms for intercept and the random effect of Sandbar*Year.

^b Difference in AIC_c scores between the model and the top fitting model in candidate set.

^c Akaike weight, representing likelihood of the model relative to others considered within the candidate set

^e Post-hoc simplification of *a priori* model.

^f Best fitting model among mechanically constructed sandbars.

Table 9. Logistic regression models and model selection results for evaluating the relationship of nest habitat on Least Tern nest fate on constructed sandbars of the Missouri River, 2006-2008.

Model Name	K ^a	ΔAIC_c^b	ω_i^c
Combination - (TerVeg - Gravel - Stems) ^d	7	0.00	0.44
Combination - (TerVeg -Stems) ^d	8	1.95	0.17
Combination - (MaxHt- TerVeg -Stems) ^d	7	2.50	0.13
Combination	10	2.87	0.10
Combination - (MaxHt- TerVeg) ^d	8	3.25	0.09
Combination.interaction	12	6.41	0.02
Natural_Habitat.interaction + Debris & Moisture	20	6.63	0.02
SandbarII ^e	8	6.95	0.01
Nest-and-Area	6	7.76	0.01
Sandbar	7	8.60	0.01
Combination Plus	13	8.69	0.01
Mechanical_Habitat	7	9.20	0.00
Mechanical_Habitat.surrounding	7	9.50	0.00
Natural_Habitat.surrounding	6	11.46	0.00
Natural_Habitat	6	12.76	0.00
Debris & Moisture	8	14.75	0.00
Mechanical_Habitat.interaction	17	19.57	0.00
Debris & Moisture Plus	17	23.27	0.00
Natural_Habitat.interaction	14	33.37	0.00
Nest	23	43.84	0.00

- ^a Number of predictors in the model, includes terms for intercept and the random effect of Sandbar*Year.
- ^b Difference in AIC_c scores between the model and the top fitting model in candidate set.
- ^c Akaike weight, representing likelihood of the model relative to others considered within the candidate set.
- ^d Post-hoc simplification of *a priori* model.
- ^e Best fitting model among natural sandbars.

Table 10. Observed means and standard deviation (SD) of continuous variables included in the best-fitting models of nest fate among constructed and natural sandbars on the Missouri River 2006-2008.

Sandbar Type Fate	Constructed		Natural	
	Failed	Successful	Failed	Successful
<i>N</i>	200	475	94	55
Pebble ^{a, b}	10.7 (13.6)	12.6 (15.2)	13.3 (23.7)	18.3 (22.6)
Cobble ^a	0.15 (0.60)	0.39 (1.57)	0 (0)	0 (0)
Sur.DebrisLrg ^b	0.82 (1.90)	0.89 (1.66)	0.93 (1.85)	1.41 (3.64)
MaxHt ^{a, b}	0.1 (0.12)	0.08 (0.12)	0.15 (0.18)	0.23 (0.31)
Sur.MaxHt ^a	0.16 (0.17)	0.13 (0.17)	0.42 (0.44)	0.38 (0.42)
Stems ^b	1.7 (5.5)	1.3 (4.7)	3.8 (7.8)	4.4 (8.1)
Sur.Stem ^a	2.2 (4.4)	1.49 (4.3)	3.8 (6.2)	3.65 (5.6)
TerVeg ^b	0.39 (0.9)	0.44 (1.3)	2.10 (5.6)	0.95 (1.2)

^a Variable included in best fitting model of nest fate among constructed sandbars

^b Variable included in best fitting model of nest fate among natural sandbars

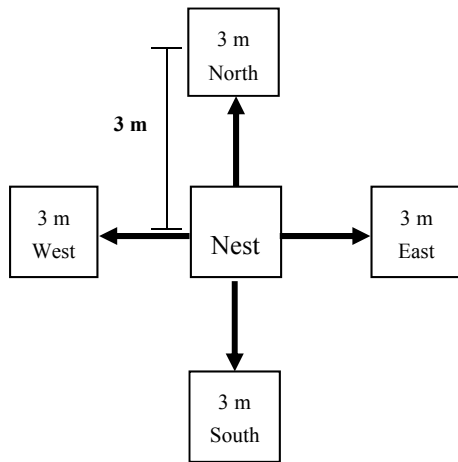


Figure 1. Schematic of nest site and 4 3-m quadrat (1-m² plots) surrounding area locations for field evaluation of nest-site and surrounding area habitat relationships (Sherfy et al. 2008).

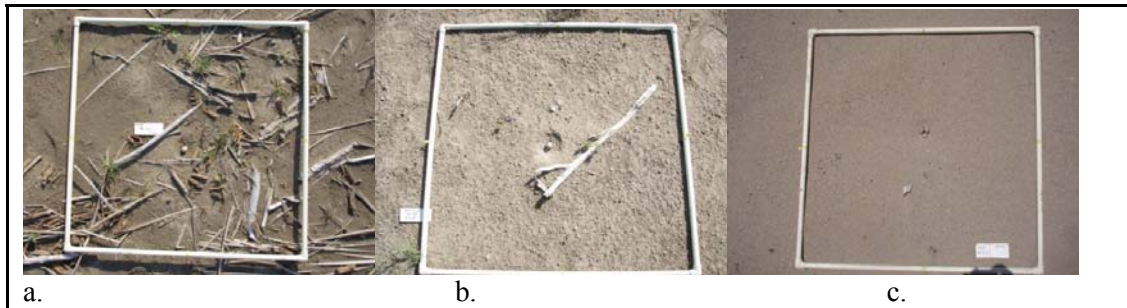


Figure. 2. Photographs demonstrating range of habitat variability at Least Tern nests on constructed sandbars at time of discovery. Each nest is surrounded by a 1-m² quadrat frame. a). Nest in wrack line, with abundant small debris, nest furniture, and limited vegetation on wet sand and silt substrate (RM 827); b) Nest with nest furniture, small debris, in contact with the nest bowl, consolidated moist sand substrate with surficial pebbles (RM 770); c) Dry, unconsolidated sand substrate (no vegetation, no debris) (RM 755).

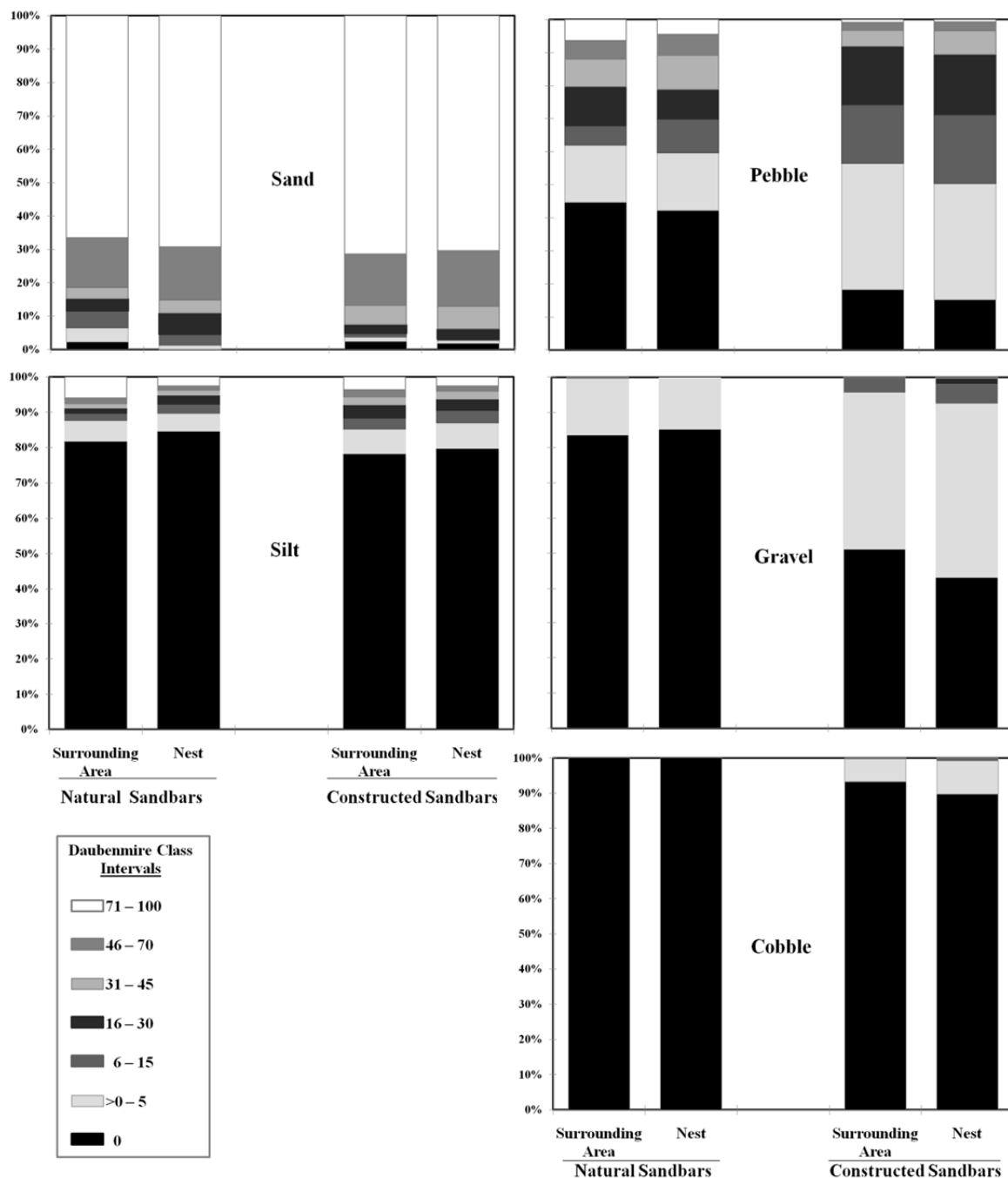


Figure 3. Substrate characteristics for Least Terns nesting on natural and constructed sandbars within the Missouri River (Gavins Point Reach, and Lewis and Clark Lake), 2006 – 2008. Results visually illustrate proportions of substrate type classifications among sampled nest sites and adjoining surrounding areas (3 m from nests) on natural and constructed sandbars.

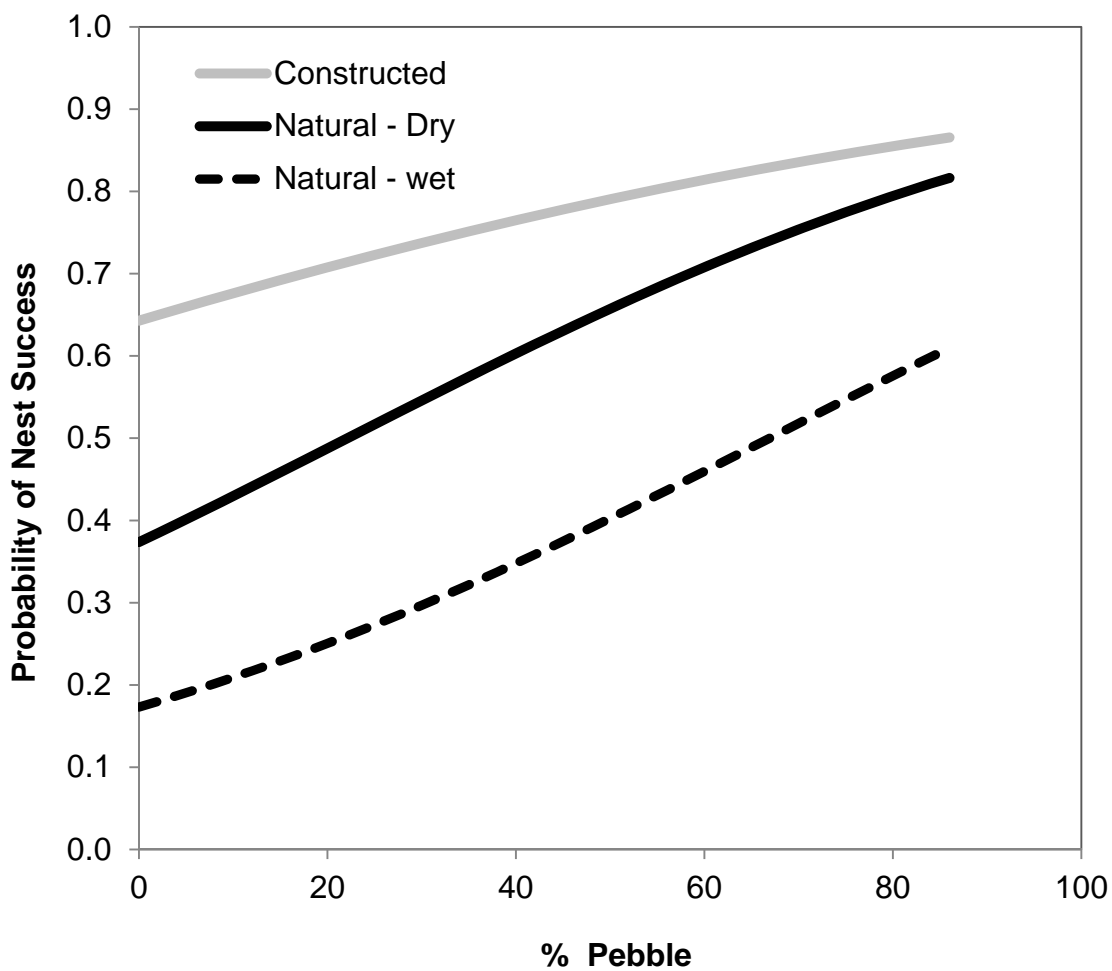


Figure 4. Increasing percentage of pebble at Least Terns nesting sites was associated with increased nest success on constructed and natural sandbars within the Missouri River (Gavins Point Reach, and Lewis and Clark Lake), 2006 – 2008. Substrate moisture differences in surrounding area (3m from nest) for natural sandbar sites are indicated by solid (dry) and wet (dashed) lines.

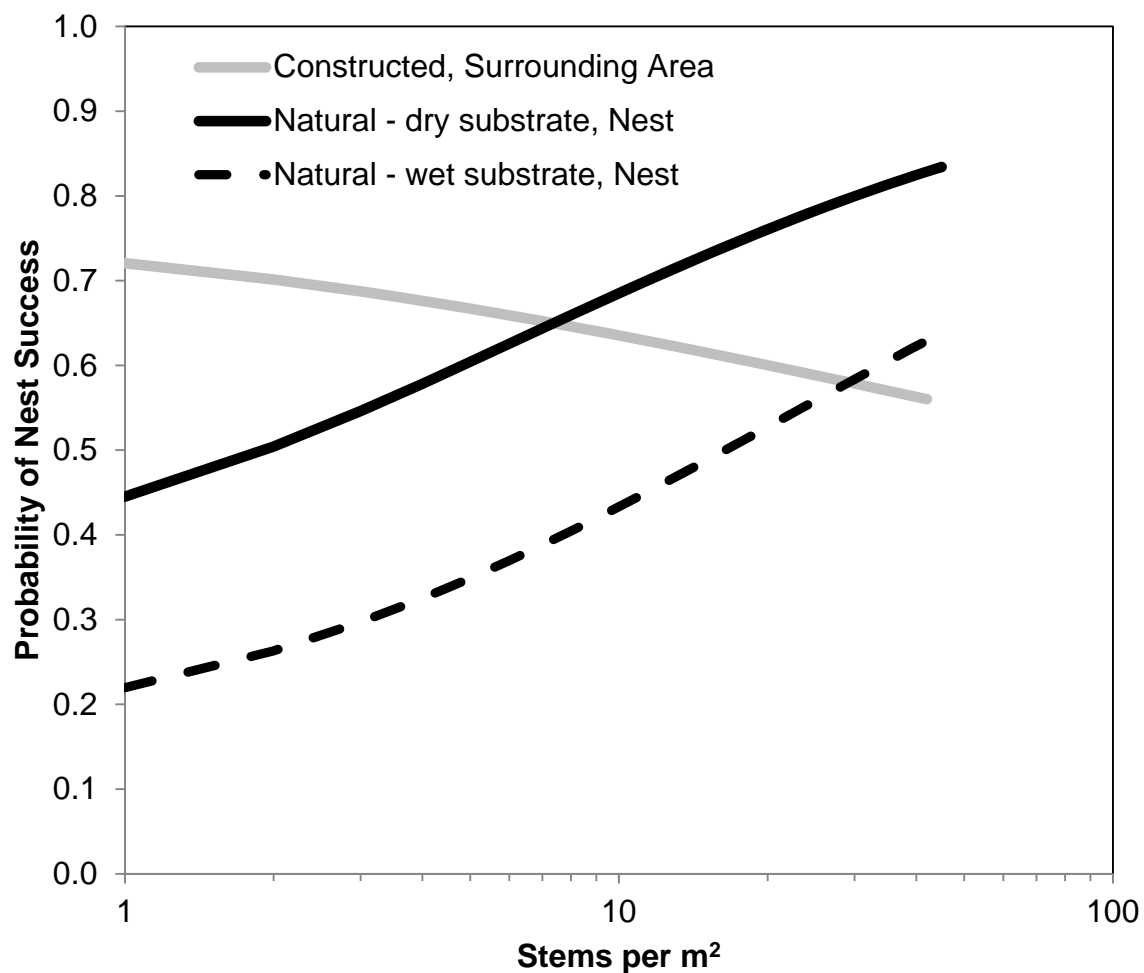


Figure 4. Stem counts were associated with Least Tern nest success within the Missouri River (Gavins Point Reach, and Lewis and Clark Lake), 2006 – 2008. Among natural sandbars increasing stem counts were associated with increased success; substrate moisture differences within surrounding area (3m from nest) are indicated by solid (dry) and wet (dashed) lines. Stem counts from the surrounding area of constructed sandbars were associated with decreased nest success.

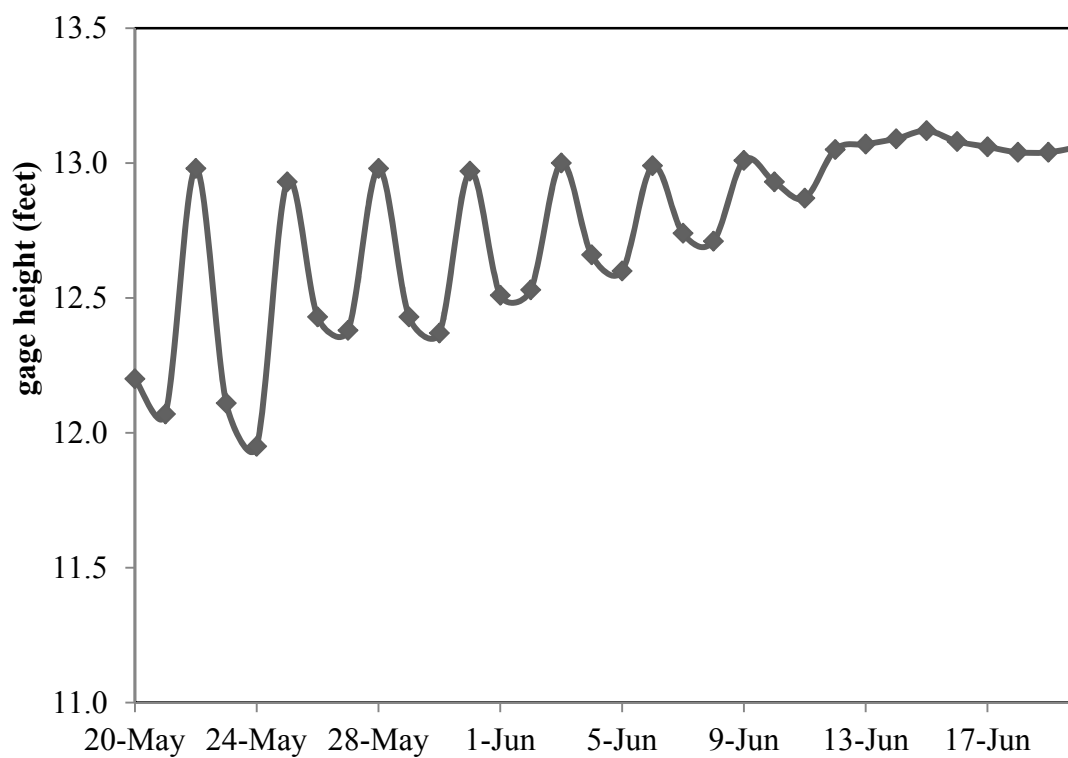


Figure 5. Typical 3-day pulsed but increasing discharge from Gavins Point Dam recorded by the Yankton, South Dakota gauge on the Missouri River, 20 May - 20 June 2006. First Least Tern nests of the season were initiated on 24 May in 2006. (Data from USGS stream gauge station 06467500).

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Chapter 3.

INFLUENCE OF HABITAT AND SCALE IN IDENTIFYING LEAST TERN (*STERNULA ANTILLARUM*) FORAGING HABITAT

Within the Missouri River, the federally endangered Interior Least Tern population (*Sternula antillarum*) appears limited by insufficient nesting habitat, typically sandbars. However, the relationship between availability of nesting habitats and required foraging habitats remains unclear. This information is needed to refine understanding of Least Tern habitat needs from a behavioral ecology perspective, and contribute to knowledge of the value of habitat restoration efforts. Our study evaluated the potential associations between specific habitat features, at differing spatial scales, associated with airborne Least Terns on the Gavins Point Reach of the Missouri River, including their use of mechanically created and natural nesting sandbars. Airborne terns are those actively within the river corridor while foraging or flying; birds flying over active colonies were not included. During 2007-2008, successful foraging sites ($N=416$) were compared to a nearby random location ($N=416$) to evaluate evidence of habitat selection during successful foraging. We also used systematic surveys in 2006-2008 to identify Least Tern airborne locations within the river corridor (2006:966 sites, 2007:2940 sites, 2008:2003 sites). Using logistic regression, we modeled the probability of the observation (random and bird) as an airborne tern based on habitat variables derived from remote sensing. To further refine our understanding of behavior in specifying habitat use, we modeled the probability of a location as a foraging site. Based on relative importance scores

derived from Akaike's Information Criteria, the variables water depth and microhabitat characteristics were most critical among successful foraging locations; turbidity and larger scale aquatic features were comparatively less important. Differences were not observed in water depth availability between natural or mechanically created habitats. Within the landscape, Least Tern airborne locations within the river corridor were best explained by multi-scale models; birds concentrated in areas with higher proportions of sandbar and wet sand habitats (within 200 m), while avoiding trees (50 m radius). When cross-validated with a reserved sample of random locations from the land cover, results suggest that in any given year, 40-97% of river corridor habitats were likely unsuitable for airborne terns. Habitat use differed by behavior; foraging birds approached nearer to wet sand patches and in areas with less emergent sandbar habitat than flying birds, with some habitat relationships differing by year. Despite the surficial visual uniformity of many aquatic habitats on the Missouri River, successful foraging by Least Terns was associated with shallow, slack-water microhabitats adjacent to emergent sandbars and within greater areas with a greater proportion of sandbar habitat. This study demonstrates the importance of incorporating both spatial scale and behavior into ecological assessments of Least Tern foraging habitats.

Several fundamental assumptions within wildlife and fisheries ecology are grounded on understanding the relationship between a species present at a location and the resources available. Linking assessments of fitness into habitat selection studies is important (Block and Brennan 1993; Clark and Shutler 1999; Jason 2001; Mayor et al. 2009) and a recent review (Gaillard et al 2010) of habitat and performance challenged investigators to link habitat assessments at various spatial-

temporal scales to appropriately scaled measures of fitness (e.g. reproduction and survival) or a performance metric (e.g. movements, such as foraging or migration). And, as advanced by Lima and Zollner (1996), many studies fail to consider animal behavior or evaluate animal perceptions of habitat during habitat and landscape assessments. Decision rules and heuristics employed by animals as they move through the environment are poorly understood at most geographic or temporal scales. Recent work demonstrates the ecological and conservation value of understanding habitat selection in light of specific behavioral requirements, nesting and foraging, while incorporating various spatial scales into the assessment (Coulombe et al. 2011).

Recently, there has been a resurgence in evaluating the importance of spatial scale when defining resource selection functions (Boyce 2006), especially to improve the habitat assessment quality and subsequent predictive value by incorporating multiple spatial scales (i.e. grain sizes) into a single model (Meyer and Thuiller 2006). Levins (1968) noted that organisms could be classified by habitat requirements as fine-grain and coarse-grain, while Johnson (1980) observed that habitat selection actually involves simultaneous selection across spatial scales, with larger scales constraining selection at finer scales. Whether modeling habitat iteratively with multiple single spatial scale models, or a single multiple spatial scale model, caution must be employed in interpretation of features correlated across scales (Battin and Lawler 2006). In a large-mammal study, Searle and colleagues (2006) observed that models including multiple spatial scale predictors better support than those that

excluded information on patch context. Among non-terrestrial taxa, modeling efforts with large river fish also supported inclusion of multiple spatial scale predictors (Poizat and Pont 1996), a finding also reported for small fish by Stucker et al. (2011) in the Missouri River.

Because many seabirds depend on prey, typically fish, distributed patchily within aquatic/marine environments, it is reasonable to expect spatially nested patterns for central-place foraging seabirds. One way to identify the important spatial scale is to identify the scale of an area-restricted search, or the tendency of an animal to focus foraging efforts among known successful patches before moving outward into new areas (Kareiva and Odell 1987). Among the largest seabirds, area-restricted searches have been defined at two distinct spatial scales, ~34 km and ~130 km, (Pinaud and Weimerskirch 2005). Selection of foraging habitat by the smaller Marbled Murrelet (*Brachyramphus marmoratus*) was associated with habitat types at scales of 10-100 km but with prey abundance at scales of <10 km; prey abundance was noted to be conditional on broader patterns of prey populations and ocean upwellings (Becker and Beissinger 2003). Therefore, although species exploit resources at the scale of microhabitat conditions (Morris 1987), those conditions are nested within larger habitat scales, which may have already constrained selection (Johnson 1980; Wiens and Rotenberry 1981; Wiens et al. 1987; Orians and Wittenberger 1991). Thus, if prey are associated with specific microhabitat features, and foraging seabirds associate habitat with prey, then highly skilled foragers may

learn to frequent specific habitats to hunt for their food (*see* (Stephens 2007).

Conversely, some habitats or features within habitats may be avoided.

Within an inland freshwater environment interrupted by terrestrial habitats, the Least Tern (*Sternula antillarum*) is an ideal species with which to evaluate the importance of spatial scale when assessing potential foraging habitats. As a surface plunging species, Least Terns are dependent on fish available within a few centimeters of the surface, and appear to specifically select narrow bodied non-spiny species <9 cm in length (Thompson et al. 1997). This smallest North American tern species nests on coastal beaches and also on sandbars and shorelines of large inland rivers (Thompson et al. 1997; Lott 2006). Least Terns nesting in coastal areas are believed to forage in near-shore habitats (Erwin 1978; Atwood and Minsky 1983), with studies of the North American interior population suggesting terns forage from <100m ((Faanes 1983) to adds far as 12 km distant from the site (Schweitzer and Leslie 1996). Characteristics of specific habitats used have varied by study and location, but include water ≤ 78 cm deep in Oklahoma (Talent and Hill 1985), and similar depth habitats and bank lines in the Mississippi River (Dugger 1997). Among areas where Least Terns nested in the Missouri River fish relative abundance increased as water depth decreased near sandbars (Stucker et al. 2011), a finding similarly reported by (Tibbs and Galat 1998). While each of these studies focuses primarily on the microhabitat of foraging sites, none addresses how Least Terns use their airborne environment and its features to select foraging habitat. It is reasonable to believe that combinations of habitat features (e.g. niche gestalt concept (James

1971; James et al. 2001), likely function as heuristics, or rules of thumb (*see* Stephens 2007), to guide movement when foraging or flying at ~30 kph (Schnell and Hellack 1979).

On the Missouri River Least Tern foraging habitats have changed substantially after the establishment of six Missouri River dams in the 1930s-1950s. Prior to dam completion the river channel was a dynamic mosaic of emergent sandbars and braided channels (Galat and Lipkin 2000; Pegg et al. 2003; Elliott and Jacobson 2006). The dams ultimately attenuated the highly dynamic flows and movement of sediment, significantly altering the ecology of the river (Galat and Lipkin 2000; Pegg et al. 2003; Galat et al. 2005; Jacobson and Galat 2008). In the mid-1980s, the quality of existing sandbar habitat for nesting and adequacy of foraging habitat was questioned by Schwalbach (1988). Although successful nesting and reproduction by Least Terns on the Missouri River was believed limited by insufficient nesting habitat (USFWS 2003), foraging habitat requirements remained unknown. In 2004, the US Army Corps of Engineers mechanically created sandbars to attract nesting Least Terns and the co-occurring Piping Plover (*Charadrius melodus*). As part of a study to determine the impact of these management actions on Least Terns, we studied the characteristics of habitats used by airborne terns in relation to the Missouri River corridor, and at a very local scale, the presence of mechanically constructed sandbars. The goal of the research was to further refine understanding of the behavior and instantaneous decision making by Least Terns within a landscape context, recognizing that some habitat features may no longer

represent natural processes in this manipulated system. Therefore, our research focused on addressing the following questions: 1) do micro-scale habitat characteristics of successful foraging locations differ from nearby random locations, and if so, how?, 2) which landscape features and spatial scales best explain Least Tern airborne locations compared to available habitats?, and 3) do differences in habitat use by behavioral state (foraging and directional flight) indicate that Least Terns employ different habitat heuristics when actively seeking food?

METHODS

Research was conducted within the ~93 km reach of the Missouri River from near Yankton, SD to Ponca, NE. This free-flowing reach of the Missouri River below the Gavins Point dam retains many of the characteristics of sandy and wide (~1 km) prairie rivers, including numerous sandbars and an active sand riverbed (Elliott and Jacobson 2006). Within the study area, data on Least Terns were collected as continuous boat-based surveys of the reach, or from boats within 15 fixed sampling areas. Sampling areas were defined during the first year of the study as bank-to-bank within an area 0.8 km upstream and downstream of sandbars used by Least Terns during the previous 5 years (G. Pavelka, U. S. Army Corps of Engineers, personal communication), or in areas where sandbars had been recently constructed for nesting habitat through mechanical means. These sampling areas were used simultaneously during the study to evaluate Least Tern nesting efforts and describe the relative abundance of prey fish, and are described in Stucker et al. (2011).

Descriptions of microhabitat conditions at Least Tern foraging locations were collected in 2007 - 2008. Concurrent with foraging behavior observations, the location of the first successful foraging observation (bird observed retrieving fish from water) was noted on a map for habitat sampling. Following the observation session, typically within 30 min, the successful foraging location and a paired random point were sampled. The random location was identified using predetermined systematic sampling locations on a 40-m grid within each sampling area using Hawth's tools (Beyer 2004) within ArcMap (9.1, ESRI, Redlands, CA, USA). Each grid point was randomly assigned a number within each sampling area, and the lowest numbered location within 200m of the successful foraging location was sampled as the paired random location. We discarded a random location during sampling if it was also an active foraging location during that behavior session, or was on land; in these situations, the next highest numbered point within 200 m was selected for the random point. At both the foraging and random sampling locations, measurements were made to describe physical habitat characteristics, including continuous and categorical variables. Continuous habitat measurements included: depth (m); turbidity (Hach 2100P, Loveland, CO, USA; nephelometric turbidity units (NTU)); substrate composition (% silt, % sand, % gravel); and presence of organic materials. Categorical habitat descriptors are spatially nested, describing the sampling location relative to the river bend (BEND habitat within surrounding ~1000-1500m; pool, channel border, bar, thalweg), position within the channel banks (CHANNEL; Sandbar, Open Water, Bankline), and in relation to the sandbars (SANDBAR; Point

Bar, Facing Bank, Facing Channel, Tail, Head, Braided Bar)(Drobish 2007).

Substrate material percentages were determined tactilely and visually. Depths >2.0 m were noted and depth estimated using an onboard sonar depth sounder. Sampling was conducted through the reproductive period, from tern nest initiation in the study area through fledging.

Least Tern locations on the river were observed and spot mapped during systematic surveys for airborne Least Terns during 2006-2008. Airborne birds were defined as those individuals observed in the air, engaged in direct flying (straight-line directional flight, head up) or actively foraging (peering downward, head-bill facing downward, hovering, diving, sinuous flight path). We surveyed regularly within a 2 week interval, allocating effort throughout daylight hours to document the location and use of habitats within the river corridor for foraging. Sampling occurred throughout the Least Tern reproductive period, from nest initiation through fledging. Systematic surveys were conducted by a crew composed of one boat driver and one observer, through a fixed length of river distance (~25-50 km per survey) at a consistent speed (6-7 km/h). Weather during the surveys was favorable, with limited wind and no precipitation or storms. Observations of birds were often made without visual assistance but from a distance, although binoculars were used for periodic scans to ensure complete coverage from shoreline to shoreline (800-1200 m). When an airborne Least Tern was observed, flying or foraging, the observer mapped the bird's location onto infrared satellite imagery from the prior year at 1:6000 - 1:7000 scales (~1.6 river-kilometers (1 river-mile)). When recording an observation, the

specific behavioral state (flying or foraging, only 2007-2008), and presence of other Least Terns, was noted, although few birds foraged in groups. Effort was made to encourage observers to map locations relative to multiple “stable” landmarks (e.g. buildings, fence rows, rip-rap) rather than annually varying sandbars. We digitized observation locations in ArcMap (9.1, ESRI, Redlands, CA, USA) using the same imagery onto which observations were recorded to ensure consistency.

GIS We created 3,000 random locations using ArcMap for sampling available habitat. Random locations were constrained to within the field sampling area of the Missouri River. For each sampling point, random or an observed tern, features believed to be important to terns were summarized to evaluate the influence of landscape attributes on tern behavioral state. These landscape elements, polygons, were identified from detailed year-specific land cover data derived from Quickbird satellite imagery and a knowledge and object-based methods (Strong et al. 2009). Attributes quantified for each point included: distances to nearest tree polygon, wet sand polygon, and river bank edge; proportions of specific habitat areas within 50 m and 200 m radii identified as water, wet sand, sandbar habitats with <30% vegetation, and trees. Prior to analysis, we transformed distance measurements using $\ln(x+1)$.

Analysis Micro-habitat data from direct field measurements of sites used by foraging Least Terns and paired random locations were analyzed to 1) evaluate if water depth differed between foraging and random locations, and 2) describe which habitat features differentiated foraging sites from those unused during the observation session. To assess if water depth differed between foraging and random locations, we

used a multinomial logistic regression (Allison 1999; Hosmer and Lemeshow 2000) categorizing depths as an ordinal response variable, while including location (foraging or random) and sandbar type (natural or created) as explanatory variables; the observation and rivermile were included as random effects. For this analysis, the continuous depths were categorized to maximize the inclusion of depth observations >2m. To evaluate the relative importance of observed habitat variables for describing foraging locations, we used a matched pairs logistic regression (Hosmer and Lemeshow 2000; Fleiss et al. 2003). We retained all data from observations with continuous depths ≤ 2 m, which resulted in unpaired observations; observations >2 m were excluded as depths as they were estimated and categorical estimates. Consequently, we reassigned unpaired observations to a “neighboring” pair (Fleiss et al. 2003). For this data set a neighboring pair was defined as in the same river mile and similar date and flow, with observations remaining unpaired, dropped from the analysis. In addition to depth, additional explanatory variables included turbidity (log transformed), percent silt, sand, gravel, and categorical landscape predictors of observation location within the river BEND, in relation to CHANNEL, and SANDBAR. Statistical assessments of these habitat features were conducted within SAS, following an information theoretic approach (Burnham and Anderson 2002) for model selection. Because we maintained no *a priori* models, all 256 possible models were run, and Akaike’s information criteria were corrected for small sample size (AIC_c). Akaike weights were computed for each model, and relative importance of

each explanatory variable was calculated by summing the Akaike weights across all 128 models in which that variable appeared.

We evaluated landscape assessments of habitat use and availability using logistic regression generalized linear mixed-effects models (lmer, package lme4 (Bates et al. 2011)) in R (R Development Core Team). We fit models incorporating a binomial distribution and a logit link function with a binary response indicating random location or bird. As we had year specific landcover data, we developed models separately for each year using 2/3 of observations (tern, random), retaining 1/3 of observations for model validation. Although we expected Least Terns to have some specific associations with landscape features, we were unclear as to the appropriate spatial scales. Because each predictor was expected to have high co-linearity across spatial scales, inclusion of a parameter only once in a model to reduce the likelihood of confounded results due to cross-scale correlations (Battin and Lawler 2006). Thus, we approached model development systematically through sequential inclusion of parameters at varying spatial scales (e.g. linear distance, proportion within 50 m, or proportion within 200m) to determine the most appropriate form for each variable. Once the best scale for a variable was determined at that step (lowest AIC value), we proceeded with inclusion of the next variable. For cases when candidate models fit equally well (within 2 AIC units), inclusion of additional parameters proceeded simultaneously in parallel. Using information-theoretic methods we distinguished among the top models using Akaike weights calculated using the small sample-size corrected AIC_c (Burnham and Anderson

2002). Inference was based on the top fitting models ($\Delta AIC_c \leq 2$), while considering the importance of inclusion/exclusion of predictors of similar models (Anderson and Burnham 2002; Arnold 2010). We report 85% confidence intervals (CI) as they are more compatible with AIC-based model selection (Arnold 2010). Once a top explanatory model was identified, its predictive ability was evaluated using the withheld data (1/3 of observations). These observations were assigned to 10 groups, based on their predicted values of y . We then found the average value of y and average \hat{y} for each group. We regressed the values of \bar{y} vs \hat{y} , seeking a positive linear relationship and high R^2 value to indicate likely predictive capacity of the top model, by year. Using the Least Tern habitat prediction models, we established probability cutpoints for each year, by plotting the intersection of model sensitivity versus specificity following Hosmer and Lemeshow (2000). This cutpoint value was then applied to the sample of withheld data to identify the proportion of habitat within the river corridor which was unlikely to be suitable for airborne Least Terns for each year.

Similarly, we evaluated further the role of behavior in refining our understanding of habitat selection by considering difference in models for two airborne behaviors (foraging, flying). Logistic regressions were again fitted using 2/3 of data from 2007 and 2008, but models followed forms identified *a priori* (Table 1) to evaluate differences in how airborne Least Terns move within their environment, based on prior studies, behavior mechanisms, or personal field observation. While variable combinations were identified prior to model fitting, the specific spatial scale

was not, and we evaluated these systematically. Employing information-theoretic methods, we distinguished among the models using Akaike weights calculated from the small sample-size corrected AIC_c (Burnham and Anderson 2002). Our inference is based on the top fitting models ($\Delta AIC_c \approx 2$), but we also considered the importance of inclusion/exclusion of individual parameters when model variables were similar (Anderson and Burnham 2002; Arnold 2010). We report 85% confidence intervals (CI) on estimates (Arnold 2010).

RESULTS

Successful foraging locations

Least Terns within the Missouri River were observed successfully foraging in very shallow waters in 2007 and 2008; 78% of the Least Tern observations were in water depths <0.5 m (Figure 1) ($F_{1,249} = 95.51, P < 0.001$). No significant difference in the depth distribution was detected among the two sandbar types, natural or mechanically created ($F_{1,42} = 0.59, P = 0.45$). The odds of recording a foraging location in shallower water (rather than deeper) is 7.6 times the odds for a random location. In the analysis including all observed habitat factors, with water depth constrained to ≤ 2 m, water depth remained the most important variable for distinguishing between foraging and random locations, followed by variables describing the foraging position in relation to the SANDBAR, CHANNEL, and substrates (Table 2). Variables that described features associated with greater landscape scales (e.g. BEND, turbidity) were comparatively less important in this analysis of successful foraging location characteristics, but 94% of foraging

observations were observed among BARS habitats, while the random points suggest 83% BARS occurrence. Among locations within SANDBAR, Braided Bar, Point Bar and Facing Bank were more associated with Least Tern foraging sites than those Facing Channel, Tail and Head (Table 2). Sandbar habitats were frequently sampled, with 40% of all random sites classified as SANDBAR-Braided Bar, but successful foraging Least Terns were observed in this habitat type in 53% of observations (Table 3).

Landscape associations of airborne Least Terns

The best supported models of habitats used by airborne Least Terns, when compared to habitats available, each included multiple spatial scales. Model parameters were relatively consistent across the three years in their direction and general magnitude of relationship among those included, although 2007 differed in the spatial scale at which variables were entered (Figs.3 – 5; Table 4-6). Furthermore, the 85% CI on parameter estimates (Table 7) support inclusion of 4-5 predictor variables in annual habitat models.

$$\begin{aligned} \text{logit}(\pi)_{2006} = & \\ & -2.29 + 13.17 \text{wetsand}_{200m} - 4.17 \text{Large.Trees}_{50m} + \\ & 2.18 \text{Sandbars}_{200m} + 1.22 \text{Water}_{50m} \end{aligned}$$

$$\begin{aligned} \text{logit}(\pi)_{2007} = & -1.94 + 13.80 \text{wetsand}_{50m} - 6.00 \text{Large.Trees}_{200m} \\ & + 4.36 \text{Sandbars}_{50m} - 4.70 \text{Water}_{50m} \end{aligned}$$

$$\begin{aligned} \text{logit}(\pi)_{2008} = & \\ & -1.1 + 4.79 \text{ wetsand}_{200m} - 7.12 \text{ Large.Trees}_{50m} + \\ & 6.85 \text{ Sandbars}_{200m} + 0.65 \text{ Water}_{50m} - 0.1 \ln(\text{Bank} + 1) \end{aligned}$$

With the landscape, airborne Least Terns generally used habitats with more wetsand and sandbar habitats, and fewer trees, than those available within this area of the Missouri River (Table 8). The sample of data used in development of models represented habitats available, as demonstrated by application of retained data to the models; visual plots of \bar{y} vs \hat{y} and formal regressions indicated strong relationships with $R^2 > 0.99$. Because models identified distribution of Least Tern airborne habitat use in relation to the distribution of available habitats, the top fitting model suggests which habitats are least likely to host airborne Least Terns. Thus, based on the best models, the proportion of unavailable habitat for airborne Least Terns was predicted to vary annually from 40-97% (Table 9).

Influence of Behavior on landscape associations Least Terns

Models contrasting Least Tern habitat use by airborne behaviors, foraging and flying, indicate subtle differences in habitat use by behavior (Figures 6-9; Table 10). Although observed means and standard deviations suggest substantial overlap among most distributions of parameters, foraging birds tended to be much closer to wetsand habitats and in areas with a reduced proportion of sandbar habitat within 200 m. Best models, as indicated by lowest AIC_c , included 4-5 predictor variables, and were supported based on 85% CI (Table 11). The simplest models, with few predictors and

only one spatial scale were not well supported, indicating that Least Tern airborne behaviors may require multiple mechanisms to explain habitat use (Tables 12-13).

$$\begin{aligned} \text{logit}(\pi)_{\text{Foraging } 2007} &= 1.68 - 0.08 \ln(\text{Wetsand} + 1) - 2.65 \text{Large.Trees}_{200m} \\ &\quad - 5.34 \text{Sandbars}_{200m} - 1.89 \text{Water}_{200m} \end{aligned}$$

$$\begin{aligned} \text{logit}(\pi)_{\text{Foraging } 2008} &= 1.61 - 0.25 \ln(\text{Wetsand} + 1) + 2.81 \text{Large.Trees}_{200m} \\ &\quad - 2.59 \text{Sandbars}_{200m} + 0.52 \text{Water}_{50m} - 0.21 \ln(\text{Bank} \\ &\quad + 1) \end{aligned}$$

Among the behavior models indicating support ($\Delta\text{AIC}_c < 2$) was a model including an interaction between linear distance to wet sand and proportion of trees within 200m ($\text{LN_Wetsand} * \text{large.trees}_{200m}$), but only for 2008. Inclusion of this interaction term in models resulted in parameter estimates in opposing directions, suggesting potential complexity and caution in interpretation of the interaction term; based on parsimony we choose the best fitting models with no interaction terms.

DISCUSSION

Our analyses indicate that Least Terns select aerial habitats at multiple spatial scales, and that habitat use is mediated by behavioral state. Direction of habitat associations was consistent across analyses, but inter-annual differences in the magnitude of the relationships were observed. In agreement with the fish sampling results (Stucker et al. 2011), no differences were observed between use or availability of shallow water near natural or mechanically created sandbars.

Successful foraging locations

Among successful foraging locations, small scale habitat use by Least Terns occurs at the scale of <20 m, and is associated with features that parallel models of fish abundance observed in the same study area (Stucker et al. 2011), particularly shallow water. Prior observations of Least Tern foraging habitat use centered on importance of water depth; our results agree with observations from Oklahoma (Talent and Hill 1985; Schweitzer and Leslie 1996), but counter observations of successful foraging in deeper waters of the Mississippi River (Dugger 1997). Shallower depths were strongly positively associated with successful foraging (this study), and increased fish abundance near the surface (Stucker et al. 2011), which should increase food availability for Least Terns. In Oklahoma Talent and Hill (1985) observed increased foraging activity in sites of high fish density, while on the Mississippi River, Tibbs and Galat (1998) found fish abundance near Least Tern colonies increased with decreasing water depth. In our study, successful foraging habitats were associated with shallower water, typically classified as sandbar margins, and zones with greater silt in the substrate composition. Silt is a feature consistent with sections of reduced current velocity (Gordon et al. 2004), typical of areas adjacent to emergent sandbars (Bowen et al. 2003). Elsewhere within the Missouri River, shallow water depths (<0.24 m) along sandbar margins were associated with abundance of fish appropriately sized for Least Terns (Ridenour 2007), and at depths similar to the observed mean water depth of successfully foraging terns in this study. Least Terns appear to preferentially forage in more complex shallow water habitats,

particularly submerged braided sandbars, and sandbar margins with slower waters, within the geomorphically and hydrologically complex Gavins Point Reach (Elliott and Jacobson 2006).

Landscape associations of airborne Least Terns

Greater scales of habitat selection (2nd and 3rd order; Johnson (1980)), based on features within the surrounding landscape, likely constrain micro-scale habitat selection (i.e. 4th order selection; successful foraging sites). As airborne Least Terns move through their environment, decisions about habitat must occur rapidly and repeatedly, and are likely based on ensuring individual safety and accessing food. Evaluating habitat selection from a large sample of moving individuals provides insight into the landscape features likely influencing the cognitive perceptions by aerial pathways available within this river corridor. In 2006 and 2008, the proportion of sandbar and wet sand habitats within a 200 m-radius were positively associated with airborne tern locations. We believe that in this analysis wet sand indicates potential for very shallow water habitats. From our field observations throughout the study, we observed that small changes in discharge in the Missouri River can readily inundate wet sand habitats, changing them into very shallow water habitats. Because shallow water depths predict fish abundance (Stucker et al. 2011), and the micro-scale foraging habitat features underscored the importance of shallow water and sandbar margins, we suggest that Least Terns may identify this habitat form as an indicator of potential foraging habitat. This finding also agrees with Faanes (1983) who observed

that birds often foraged near nesting sandbars on the Platte River. While not all sandbars included in this study had suitable habitat for Least Tern nesting, those with an abundance of wet sand habitat would still support foraging habitat.

At a slightly smaller scale, within a 50 m-radius, tern habitat is associated with reduced proportions of trees, indicating some degree of avoidance. Trees are not foraging habitat for terns, and may present a physical hazard to flight and potentially a location harboring aerial predators. In this portion of the Missouri River, most of the trees identified from the remote sensing were mature and were located within the flood plain or on higher elevation islands characterized by cut banks. Therefore, while terns avoid trees, this effect may be intensified by co-occurring river bank scouring processes and associated areas of deeper water, which are also unlikely successful foraging habitats. Biologically, it is reasonable for Least Terns to avoid areas with trees. However, tree avoidance becomes complicated when behavior is included in the models.

Incorporating specific behaviors into Least Tern airborne habitat models is warranted. While the behavior specific habitat models did not differ as greatly as those modeling use and availability, subtle insights were gleaned from models incorporating behavior. Models differed by year in the magnitude of the model estimates, likely in relation to the landcover data quality, but there was consistency across years in the direction of the relationships. For example, foraging birds consistently minimized their distance to wet sand habitats but stayed away from areas with greater proportions of sandbar habitats when compared to flying birds.

Although differences by year were found in response to trees, we suspect that foraging birds are more likely to approach areas with greater proportions of trees than flying individuals, also evidenced in part, by terns flying near riverbanks. While evidence of foraging in the context of fear (*see* review by Brown and Kotler (2007)) is difficult to obtain in a purely observational study, we propose that foraging terns are willing to access foraging habitats near trees and banks, if the habitats meet the needs of terns; in this situation, we believe that need is shallow water habitats with available prey fish.

Models are limited by the data used to build them, whether observations of terns or the landcover data incorporated into the effort. Habitat models that rely solely on observations of flying terns will be more constrained in predicting habitat use than those that incorporate foraging and flying data. Investigators seeking true estimates of foraging habitat use may need to limit observations to actively foraging individuals, rejecting observations of terns in directional flight, in particular. For these landscape models, we depended on consistent identification of features observed remotely from satellite imagery in conjunction with object identification (Strong et al. 2009). Difficulty in accurate interpretation due to acquisition quality, river discharge, or time relative to use potentially obscured our understanding of habitat use and availability. General consistency among scale and parameter estimates in 2006 and 2008, as compared to 2007, indicates the importance of timely and accurate imagery interpretation for landscape level model development; >50% of 2007 imagery was obtained in October after the breeding season when flow differed

considerably to the nesting season. The 2007 landscape scale models differed substantially from 2006 or 2008, particularly in the scale at which parameters entered the model. This difference suggests that interpretation of the water–wetsand–sandbar habitats in that year may have been compromised and may not reflect the true availability of habitats during the nesting season. Identification of shoreline, the water and terrestrial interface, is known to be difficult (Stockdonf et al. 2002). Advances in accurate landcover interpretation from Quickbird imagery (Strong et al. 2009) was demonstrated in the consistency of the models from 2006 and 2008. This analysis underscores the importance of accurate identification of these habitats, and careful consideration of inundation corrections for identifying shallowly inundated and barely emergent habitats. Although the 2007 models are statistically well supported based on 85% CI, we are more confident in biological interpretation of the 2006 and 2008 models, particularly in the similarity of parameter estimates, despite substantially different flow and sandbar habitat availability in those years. Consequently, we suggest that resulting 2007 estimate of 97% river corridor habitats as unavailable for airborne Least Terns is inflated. Yet if the 2006 and 2008 models are more reasonable, then potential exists for 40-70% of riverine habitats to be unsuitable to airborne Least Terns. If those estimates are further constrained by micro-scale habitat requirements associated with prey availability, which is strongly associated with shallow water depth, then estimates of profitable foraging habitats will be substantially reduced. Although this analysis used wet sand as a proxy for shallow water habitat, its accuracy and the level of bias is unclear. Broad scale

estimates of water depth from remote sensing, direct field measurements, or via modeling in a highly dynamic river system, like the Missouri, are exceedingly difficult to obtain due to scale of area, system and flow complexity. While future estimates of habitat can likely be obtained from landcover data, digital elevation models and fine scale bathymetric models will better refine the amount of habitat truly “available” to Least Terns.

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Table 1. *A priori* model families, parameters, and expected direction of relationship for evaluating habitats of flying and foraging Least Terns.

Model Family	Parameters	Model Origin
1	Wetsand	Fish abundance is associated with shallow water (Stucker et al. 2011) thus foraging birds are more associated shallow water; wetsand used as proxy for shallow water; Least Tern foraging associated with shallow water (Hill) (Talent and Hill 1985)
2	Tree	Trees may be direct and indirect hazard to flying terns. All airborne terns should maximize distance from trees, little habitat difference between airborne terns exhibiting foraging or flying behavior.
3	River bank	Least Terns forage along riverbanks (Dugger 1997); foraging birds should be closer than flying birds
4	Wetsand*Trees	Foraging Least Terns make tradeoffs to access shallow water areas near trees. Foraging terns optimize proximity to trees and shallow water (wet sand), while flying terns will use wet sand habitats only that maximize distance from trees.
5	Sandbars+wetsand	Least Terns forage off of nesting areas (Faanes 1983), therefore differential use, preference by foraging terns,

Model Family	Parameters	Model Origin
		but not flying birds.
6	Water	All water is foraging habitat; therefore areas with greater proportions of water should have greater likelihood of foraging.
7	Sandbars + Trees + Wetsand + Water + Bank	Foraging habitats are multi-scale and context specific; similar to this study, habitat selection models.

Table 2. Habitat features associated with successful Least Tern foraging sites among water depths ≤ 2 m, ranked by AIC relative importance values, estimates of β and unconditional standard errors, and observed means with standard deviation for foraging and random locations.

Variable	AIC Relative			Foraging	Random
	Importance	β	SE	mean	mean
	Values			(SD)	(SD)
Water Depth	1.000			0.31	0.64
(m)		-2.83	0.53	(0.31)	(0.48)
SANDBAR	0.942				
<i>Braided bar</i>		<i>(baseline)</i>	--		
Point Bar		2.19	0.92		
Facing					
Bank		0.67	0.48		
Facing					
Channel		-0.61	0.48		
Tail		-0.89	0.55		
Head		-1.58	0.85		
CHANNEL	0.730				
<i>Bankline</i>		<i>(baseline)</i>	--		
Sandbar		-0.68	0.44		
Open					
Water		0.02	0.60		

Variable	AIC Relative Importance Values	β	SE	Foraging mean (SD)	Random mean (SD)
Percent Silt	0.376	0.01	0.01	31 (38)	21 (33)
Percent Gravel	0.361	-0.01	0.01	5 (16)	6 (20)
Percent Sand	0.345	0.00	0.01	62 (40)	72 (38)
Turbidity (NTU)	0.269	0.01	0.10	39 (30)	37 (18)
BEND	0.108				
<i>Thalweg</i>		<i>(baseline)</i>	--		
Bars		-0.08	0.11		
Channel					
Border		-0.05	0.09		
Pool		0.22	0.24		

Table 3. Categorical classification of habitats and proportion of all observations with waterdepth ≤ 2 m included in the matched pairs logistic regression analysis of successfully foraging Least Terns ($n = 228$) and nearby random locations ($n=188$) in the Missouri River.

BEND	CHANNEL	SANDBAR	SAMPLING LOCATION	
			Foraging	Random
Bars	Sandbar	Point Bar	0.04	0.02
		Facing Bank	0.12	0.10
		Facing Channel	0.11	0.13
		Tail	0.05	0.07
		Head	0.03	0.04
		Braided bar	0.53	0.40
	Open Water	Head	0.00	0.04
	Bankline	Point Bar	0.01	0.00
		Facing Bank	0.01	0.00
		Tail	0.04	0.03
Channel border	Sandbar	Point Bar	0.01	0.01
		Facing Bank	0.00	0.01
		Facing Channel	0.00	0.01
	Open Water	Facing Channel	0.00	0.01
		Head	0.01	0.03
	Bankline	Facing Bank	0.00	0.01

BEND	CHANNEL	SANDBAR	SAMPLING LOCATION	
			Foraging	Random
		Tail	0.00	0.01
Pool	Sandbar	Facing Bank	0.00	0.01
	Open Water	Head	0.00	0.01
	Bankline	Tail	0.00	0.00
Thalweg	Sandbar	Head	0.00	0.01
	Open Water	Facing Bank	0.00	0.00
		Head	0.01	0.07
	Bankline	Facing Bank	0.01	0.01
		Tail	0.00	0.00

Table 4. Results of 2006 logistic regression multi-scale habitat models for airborne Least Terns on the Missouri River. Model development was based on 2644 observations (2000 random, 644 LETE). Numbers prior to variable indicate systematic steps for identifying appropriate spatial scale for variable inclusion.

2006 Least Tern Habitat Model	K^a	AIC_c^b	ΔAIC_c^c	ω_i^d
3c) Wetsand_200m + Large.trees_50m + Sandbar_200m + Water_50m	5	2648.2	0.0	0.77
4) Wetsand_200m + Large.trees_50m + Sandbar_200m + Water_50m + LN_Bank	6	2650.1	1.9	0.23
3b) Wetsand_200m + Large.trees_50m + Sandbar_50m + Water_50m	5	2657.7	9.5	0.00
2b) Wetsand_200m + Large.trees_50m + Sandbar_50m	4	260.0	31.8	0.00
3a) Wetsand_200m + Large.trees_50m + Sandbar_50m + Water_200m	5	2681.4	33.2	0.00
1b) Wetsand_200m + Large.trees_50m	3	2682.2	34.0	0.00
2a) Wetsand_200m + Large.trees_50m + Sandbar_200m	4	2684.0	35.8	0.00
1a) Wetsand_50m + Large.trees_200m	3	2748.5	100.3	0.00

^a Number of predictors in the model, includes terms for intercept.

^b Akaike's Information Criterion, corrected for small sample size

^c Difference in AIC_c scores between the model and the top fitting model in candidate set.

^d Akaike weight, representing likelihood of the model relative to others considered within the candidate set.

Table 5. Results of 2007 logistic regression multi-scale habitat models for airborne Least Terns on the Missouri River. Model development was based on 3960 observations (2000 random, 1960 LE7E). Numbers prior to variable indicate systematic comparisons for identifying appropriate spatial scale for variable inclusion.

2007 Least Tern Habitat Model	K^a	AIC_c^b	ΔAIC_c^c	ω_i^d
3b) Wetsand_50m + Large.trees_200m + Sandbar_50m + Water_50m	5	636.7	0.00	0.50
4) Wetsand_50m + Large.trees_200m + Sandbar_50m + Water_50m + LNBank	6	636.7	0.03	0.50
2d) Wetsand_50m + Large.trees_200m + Sandbar_50m	4	784.8	148.1	0.00
3a) Wetsand_50m + Large.trees_200m + Sandbar_50m + Water_200m	5	785.1	148.4	0.00
2c) Wetsand_50m + Large.trees_50m + Sandbar_50m	4	786.9	150.2	0.00
2b) Wetsand_50m + Large.trees_50m + Sandbar_200m	4	1085.8	449.1	0.00
2a) Wetsand_50m + Large.trees_200m + Sandbar_200m	4	1091.0	454.3	0.00
1a) Wetsand_50m + Large.trees_200m	3	1167.2	530.5	0.00
1b) Wetsand_200m + Large.trees_50m	3	4801.6	4164.9	0.00

^a Number of predictors in the model, includes terms for intercept.

^b Akaike's Information Criterion, corrected for small sample size

^c Difference in AIC_c scores between the model and the top fitting model in candidate set.

^d Akaike weight, representing likelihood of the model relative to others considered within the candidate set.

Table 6. Results of 2008 logistic regression multi-scale habitat models for airborne Least Terns on the Missouri River. Model development was based on 3335 observations (2000 random, 1335 LE/TE). Numbers prior to variable indicate systematic comparisons for identifying appropriate spatial scale for variable inclusion.

2008 Least Tern models	K^a	AIC_c^b	ΔAIC_c^c	ω_i^d
4) Wetsand_200m + Large.trees_50m + Sandbar_200m + Water_50m + LN_Bank	6	3806.3	0.0	0.72
3b) Wetsand_200m + Large.trees_50m + Sandbar_200m + Water_50m	5	3808.7	2.4	0.28
3a) Wetsand_200m + Large.trees_50m + Sandbar_200m + Water_200m	5	3819.6	13.3	0.01
2b) Wetsand_200m + Large.trees_50m + Sandbar_200m	4	3835.1	28.8	0.00
2a) Wetsand_200m + Large.trees_50m + Sandbar_50m	4	3967.5	161.2	0.00
1b) Wetsand_200m + Large.trees_50m	3	4113.9	307.6	0.00
1a) Wetsand_50m + Large.trees_200m	3	4238.3	432.0	0.00

^a Number of predictors in the model, includes terms for intercept.

^b Akaike's Information Criterion, corrected for small sample size

^c Difference in AIC_c scores between the model and the top fitting model in candidate set.

^d Akaike weight, representing likelihood of the model relative to others considered within the candidate set.

Table 7. Confidence intervals, 85%, of model coefficients (β) for best models predicting airborne Least Tern habitats on the Missouri River 2006-2008.

	Lower	Upper
2006		
Wetsand_200m	10.98	15.36
Large.trees_50m	-5.88	-2.45
Sandbar_200m	1.23	3.13
Water_50m	0.91	1.52
2007		
Wetsand_50m	12.62	14.99
Large.trees_200m	-8.03	-3.96
Sandbar_50m	3.71	5.02
Water_50m	-5.41	-4.00
2008		
Wetsand_200m	4.12	5.45
Large.trees_50m	-9.43	-4.82
Sandbar_200m	6.20	7.50
Water_50m	0.47	0.82
Bank distance (ln)	-0.17	-0.03

Table 8. Mean, standard deviation (σ), and back-transformed mean [] values of continuous variables included in the best-fitting models of airborne Least Tern habitats on the Missouri River 2006-2008.

	2006		2007		2008	
	Random	Tern	Random	Tern	Random	Tern
Sandbar	b 0.031 (0.082)	b 0.055 (0.087)	a 0.031 (0.101)	a 0.09 (0.175)	b 0.049 (0.088)	b 0.140 (0.150)
Large Trees	a 0.070 (0.186)	a 0.007 (0.025)	b 0.081 (0.138)	b 0.023 (0.047)	a 0.033 (0.099)	a 0.004 (0.020)
Water	a 0.693 (0.403)	a 0.812 (0.231)	a 0.674 (0.406)	a 0.058 (0.111)	a 0.579 (0.420)	a 0.558 (0.357)
Wet sand	b 0.008 (0.024)	b 0.035 (0.079)	a 0.015 (0.056)	a 0.738 (0.289)	b 0.049 (0.084)	b 0.104 (0.104)
In Bank Distance					5.145 (1.013)	5.415 (0.858)
					[171 m]	[224 m]

^a proportion within 50m, ^b proportion within 200m

Table 9. Best multi-scale airborne Least Tern habitat model, by year, including \bar{y} vs \hat{y} R^2 values, cut-points, with percent of random habitat locations predicted to fall below expected cut-point.

Year	\bar{y} vs \hat{y} R^2	Cutpoint value	Predicted % of habitat unavailable
2006	0.99	0.24	40%
2007	0.99	0.43	97%
2008	0.99	0.35	70%

Table 10. Mean, standard deviation (σ), and back-transformed mean μ of continuous variables included in the best-fitting models identifying probabilities of airborne Least Terns as demonstrating behaviors of foraging or flying on the Missouri River 2007-2008.

	2007		2008	
	Flying	Foraging	Flying	Foraging
Sandbar_200m	0.095 (0.047)	0.084 (0.048)	0.168 (0.173)	0.105 (0.104)
Large.trees_200m	0.022 (0.047)	0.025 (0.048)	0.016 (0.041)	0.026 (0.053)
Water	μ 0.057 (0.105)	σ 0.060 (0.119)	μ 0.522 (0.379)	σ 0.603 (0.321)
Wetsand distance (ln)	3.588 (1.561)[35m]	3.5 (1.484)[32m]	3.086 (1.563) [21m]	2.844 (1.603) [16m]
Bank distance (ln)			5.521 (0.765)	5.281 (0.948)
			[249m]	[196m]

^a proportion within 50m

^b proportion within 200m

Table 11. Confidence intervals, 85%, of model coefficients (β) for best habitats models predicting probability of Least Tern foraging on the Missouri River 2007-2008.

	Lower	Upper
2007		
Sandbar_200m	-6.38	-4.30
Large.Trees_200m	-4.29	-1.00
Water_200m	-2.31	-1.46
Wetsand distance (ln)	-0.13	-0.03
2008		
Sandbar_200m	-3.36	-1.82
Large.Trees_200m	0.53	5.08
Water_50m	0.22	0.81
Wetsand distance (ln)	-0.31	-0.19
Bank distance	-0.33	-0.08

Table 12. Results of 2007 logistic regression multi-scale habitat models for foraging and flying Least Terns on the Missouri River. Model development based on 1960 observations (871 flying, 1143 foraging).

Family	Bird Behavior Models	K ^a	AIC _c ^b	ΔAIC _c ^c	ω _i ^d
6 ^e	LN_Wetsand + large.trees_200m + Sandbar_200m + Water_200m	5	2602.4	0.00	0.37
6	LN_Wetsand * large.trees_200m + Sandbar_200m + Water_200m	6	2603.34	0.91	0.22
6	LN_Wetsand + large.trees_200m + Sandbar_200m + Water_200m + LN_Bank	6	2603.84	1.41	0.17
6	LN_Wetsand + Sandbar_200m + Water_200m	4	2605.9	3.49	0.06
6	LN_Wetsand + LN_Tree + Sandbar_200m + Water_200m	5	2606.6	4.20	0.04
6	LN_Wetsand + large.trees_50m + Sandbar_200m + Water_200m	5	2606.9	4.50	0.04
6	Wetsand_200m + large.trees_200m + _200m + Water_200m	5	2607.8	5.40	0.02
6	Wetsand_50m + large.trees_200m + Sandbar_200m + Water_200m	5	2608.4	6.00	0.02
6	LN_Wetsand * LN_Tree + Sandbar_200m + Water_200m,	6	2608.64	6.21	0.02
6	LN_Wetsand + LN_Tree + Sandbar_200m	4	2631.9	29.49	0.00
6	LN_Wetsand + LN_Tree + Sandbar_200m + Water_50m	5	2633.8	31.40	0.00
5 ^e	Sandbar_200m + LN_Wetsand	3	2640.51	38.08	0.00

Family	Bird Behavior Models	K ^a	AIC _c ^b	ΔAIC _c ^c	ω _i ^d
5	Wetsand_200m + Sandbar_200m	3	2646.81	44.38	0.00
6	LN_Wetsand + LN_Tree + Sandbar_50m	4	2650.02	47.59	0.00
4 ^e	LN_Wetsand + LN_Tree	3	2650.11	47.68	0.00
4	LN_Wetsand * LN_Tree	4	2652.12	49.69	0.00
2 ^e	LN_Tree	2	2653.41	50.98	0.00
3 ^e	LN_Bank	2	2655.61	53.18	0.00
6	Water_200	2	2656.91	54.48	0.00
5	Wetsand_50m + Sandbar_50m	3	2663.41	60.98	0.00
2	Tree_50	2	2664.81	62.38	0.00
4	LN_Wetsand + large.trees_50m	3	2664.91	62.48	0.00
1 ^e	LN_Wetsand	2	2665.11	62.68	0.00
2	Tree_200	2	2665.41	62.98	0.00
6	Water_50	2	2666.11	63.68	0.00
1	Wetsand_200	2	2666.41	63.98	0.00

Family	Bird Behavior Models	K ^a	AIC _c ^b	Δ AIC _c ^c	ω_i ^d
4	Wetsand_200m + large.trees_50m	3	2666.51	64.08	0.00
1	Wetsand_50	2	2666.61	64.18	0.00
4	Wetsand_50m +large.trees_200m	3	2667.41	64.98	0.00

^a Number of predictors in the model, includes terms for intercept.

^b Akaike's Information Criterion, corrected for small sample size

^c Difference in AIC_c scores between the model and the top fitting model in candidate set.

^d Akaike weight, representing likelihood of the model relative to others considered within the candidate set.

^e Top ranked model within model family.

Table 13. Results of 2008 logistic regression multi-scale habitat models for foraging and flying Least Terns on the Missouri River. Model development based on 1335 observations (745 flying, 590 foraging).

Family	Bird Behavior Models	K ^a	AIC _c ^b	ΔAIC _c ^c	ω _i ^d
6 ^e	LN_Wetsand + Large.Trees_200m + Sandbar_200m + water_50m + LN_Bank	6	1739.6	0.00	0.35
6	LN_Wetsand + Sandbar_200m + water_50m + LN_Bank	5	1740.7	1.18	0.19
6	LN_Wetsand * Large.Trees_200m + Sandbar_200m + water_50m + LN_Bank	7	1740.8	1.22	0.19
6	LN_Wetsand + LN_Large.Tree + Sandbar_200m + water_50m + LN_Bank	6	1741.8	2.20	0.12
6	LN_Wetsand + Large.Trees_50m + Sandbar_200m + water_50m + LN_Bank	6	1742.6	3.00	0.08
6	LN_Wetsand * LN_Large.Tree + Sandbar_200m + water_50m + LN_Bank	7	1742.8	3.22	0.07
6	LN_Wetsand + LN_Large.Tree + Sandbar_200m + water_50m	5	1746.6	7.08	0.01
6	LN_Wetsand + LN_Large.Tree + Sandbar_200m + water_200m	5	1749.9	10.38	0.00
5 ^e	LN_Wetsand + LN_Large.Tree + Sandbar_200m	4	1751.6	12.07	0.00
5	LN_Wetsand + LN_Large.Tree + Sandbar_50m	4	1754.9	15.37	0.00
5	Sandbar_200m + LN_Wetsand	3	1755.12	15.55	0.00
5	wetsand_200m + Sandbar_200m	3	1762.92	23.35	0.00

Family	Bird Behavior Models	K ^a	AIC _c ^b	ΔAIC _c ^c	ω _i ^d
5	wetsand_200m + Sandbar_200m	3	1771.52	31.95	0.00
5	wetsand_50m + Sandbar_50m	3	1776.22	36.65	0.00
4 ^e	LN_Wetsand + LN_Large.Tree	3	1808.9	69.35	0.00
4	LN_Wetsand * Large.Trees_200m	4	1810.13	70.57	0.00
4	LN_Wetsand * LN_Large.Tree	4	1810.43	70.87	0.00
3 ^e	LN_Bank	2	1810.81	71.25	0.00
4	wetsand_50m + LN_Large.Tree	3	1815.5	75.95	0.00
4	wetsand_50m + Large.Trees_200m	3	1817.0	77.45	0.00
6	Water 50	2	1819.51	79.95	0.00
2 ^e	Large.Tree_200	2	1821.91	82.35	0.00
2	LN_Large.Tree	2	1822.71	83.15	0.00
1 ^e	LN_Wetsand	2	1829.01	89.45	0.00
1	Wetsand_50	2	1833.01	93.45	0.00
1	Wetsand_200	2	1834.71	95.15	0.00

Family	Bird Behavior Models	K ^a	AIC _c ^{a, b}	Δ AIC _c ^c	ω_i ^d
4	wetsand_200m + Large.Trees_50m	3	1835.8	96.25	0.00
3	Large.Tree_50	2	1836.21	96.65	0.00
6	Water 200	2	1836.61	97.05	0.00

^a Number of predictors in the model, includes terms for intercept.

^b Akaike's Information Criterion, corrected for small sample size

^c Difference in AIC_c scores betweenf the model and the top fitting model in candidate set.

^d Akaike weight, representing likelihood of the model relative to others considered within the candidate set.

^e Top ranked model within model family.

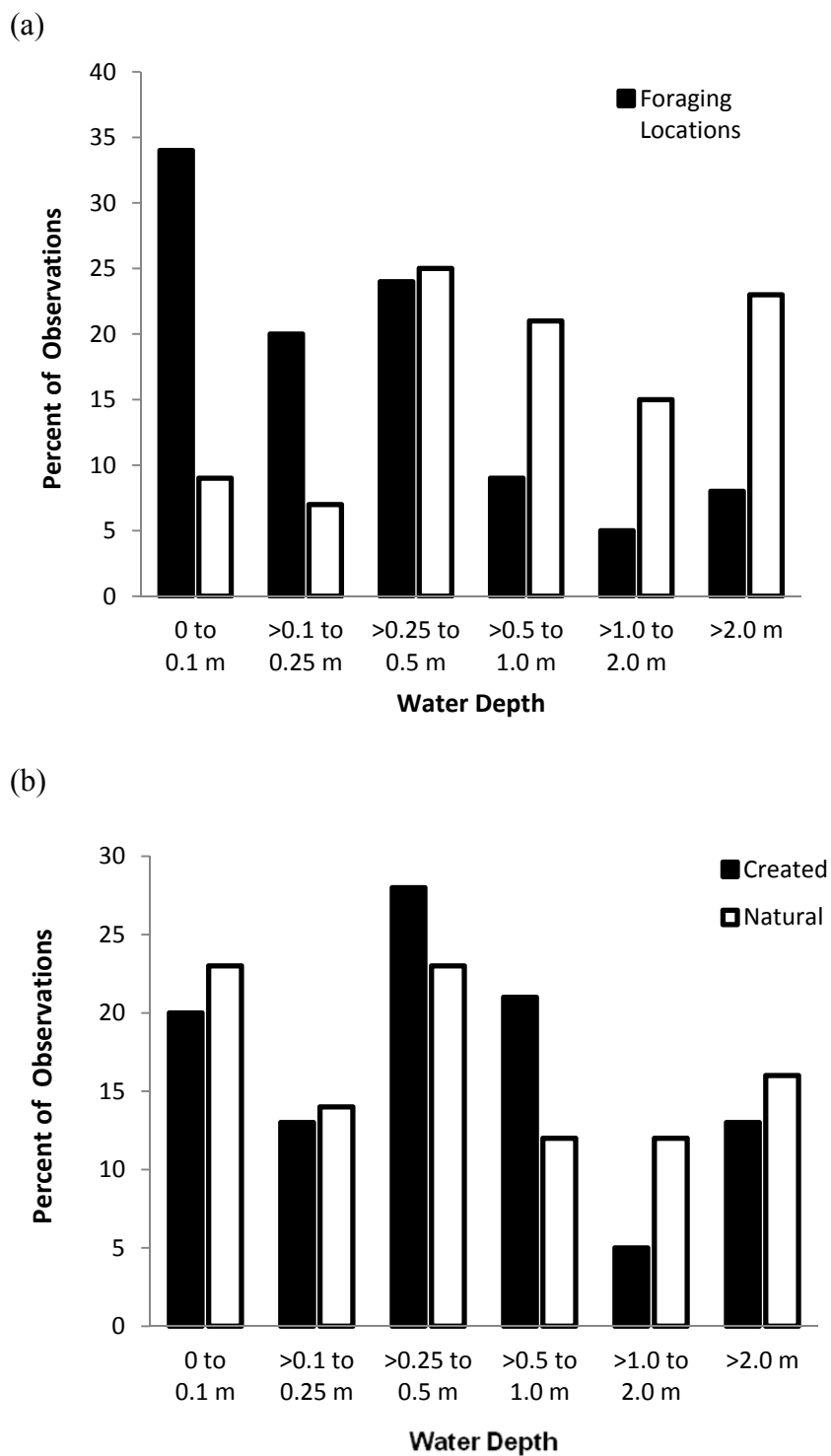


Figure 1. Proportion of observations, by depth, for (a) foraging and random locations, and (b) mechanically created and natural sites.

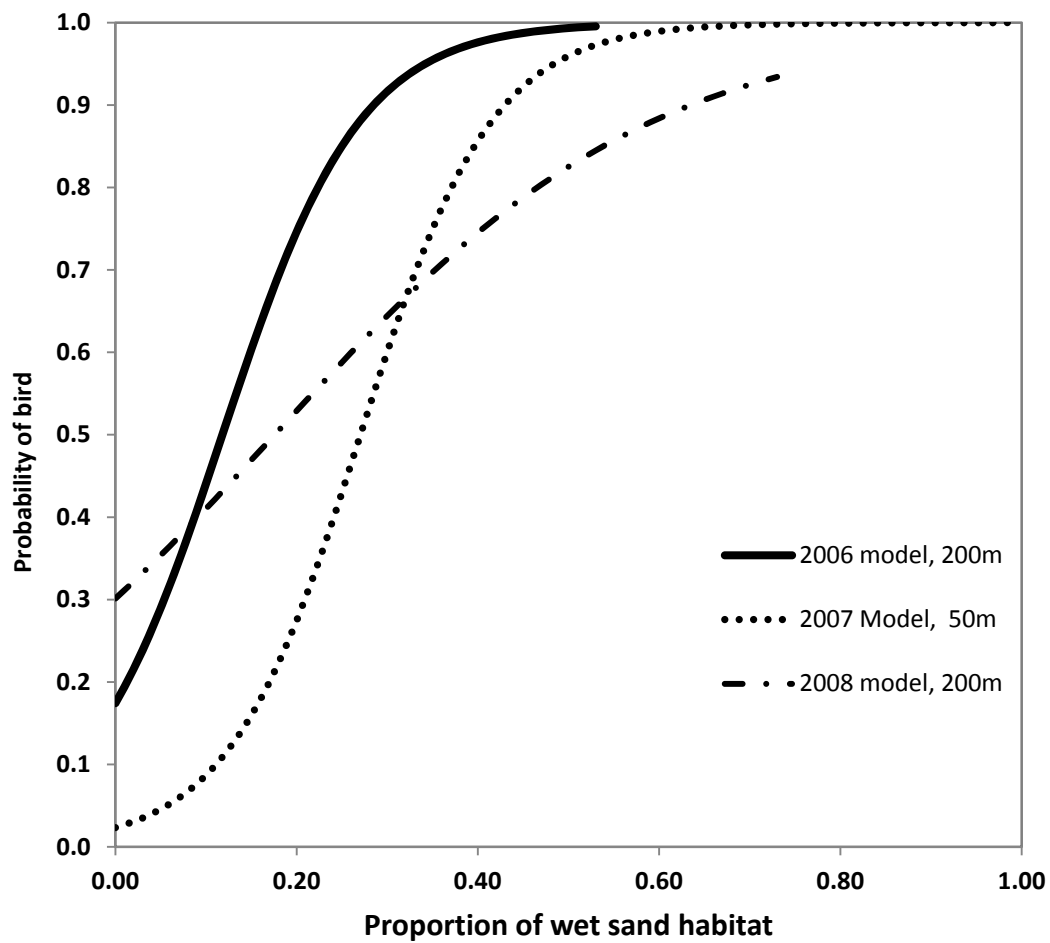


Figure 2. The proportion of wet sand habitats within 50m or 200m and probability of bird use as predicted by best model for each year.

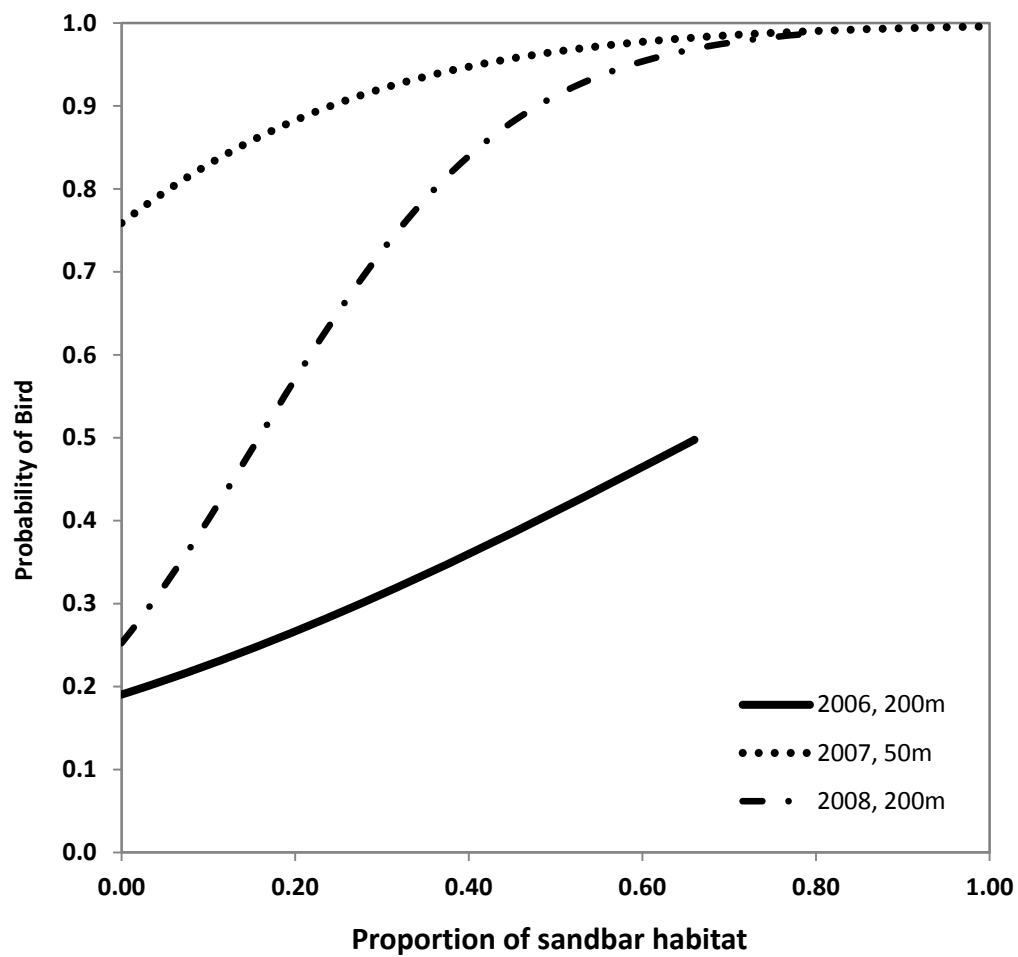


Figure 3. The proportion of sandbar nesting habitats within 50m or 200m and probability of bird use as predicted by best model for each year.

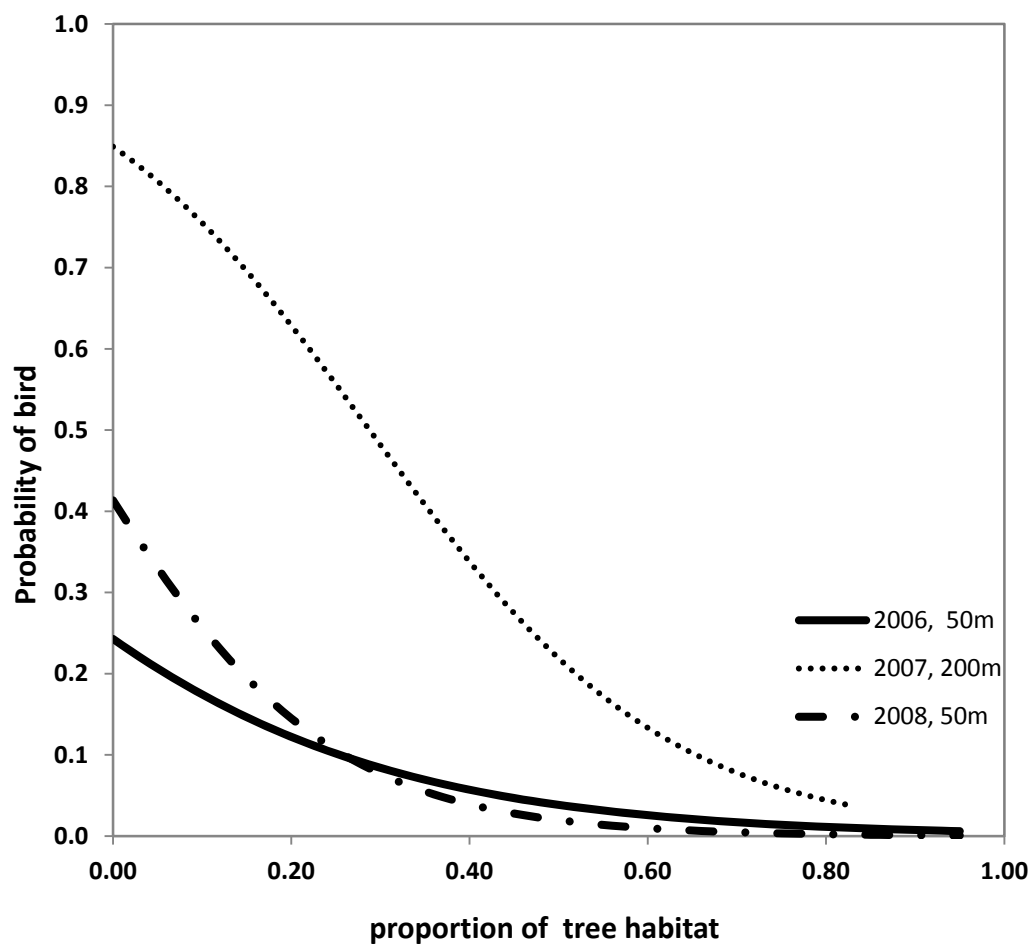


Figure 4. The proportion of large tree habitats within 50m or 200m and probability of bird use as predicted by best model for each year.

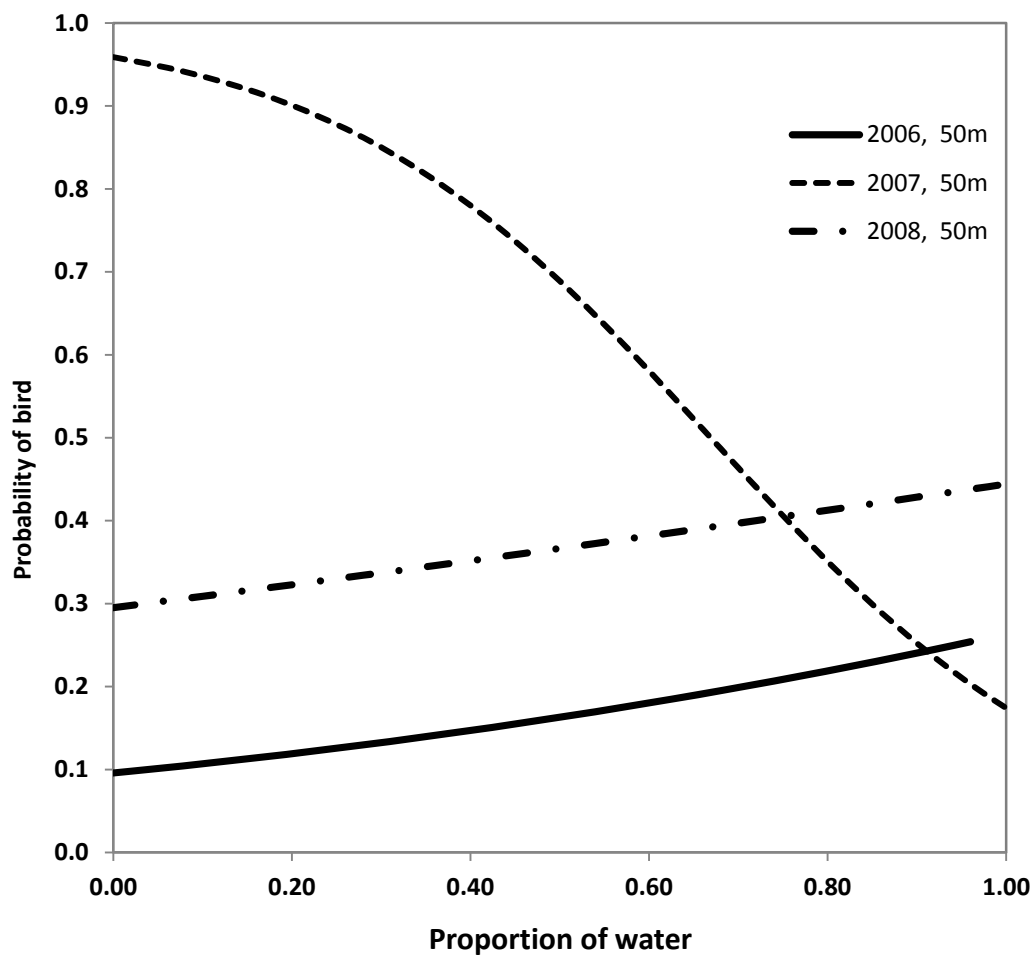


Figure 5. The proportion of water within 50m and the probability of bird use as predicted by best model for each year.

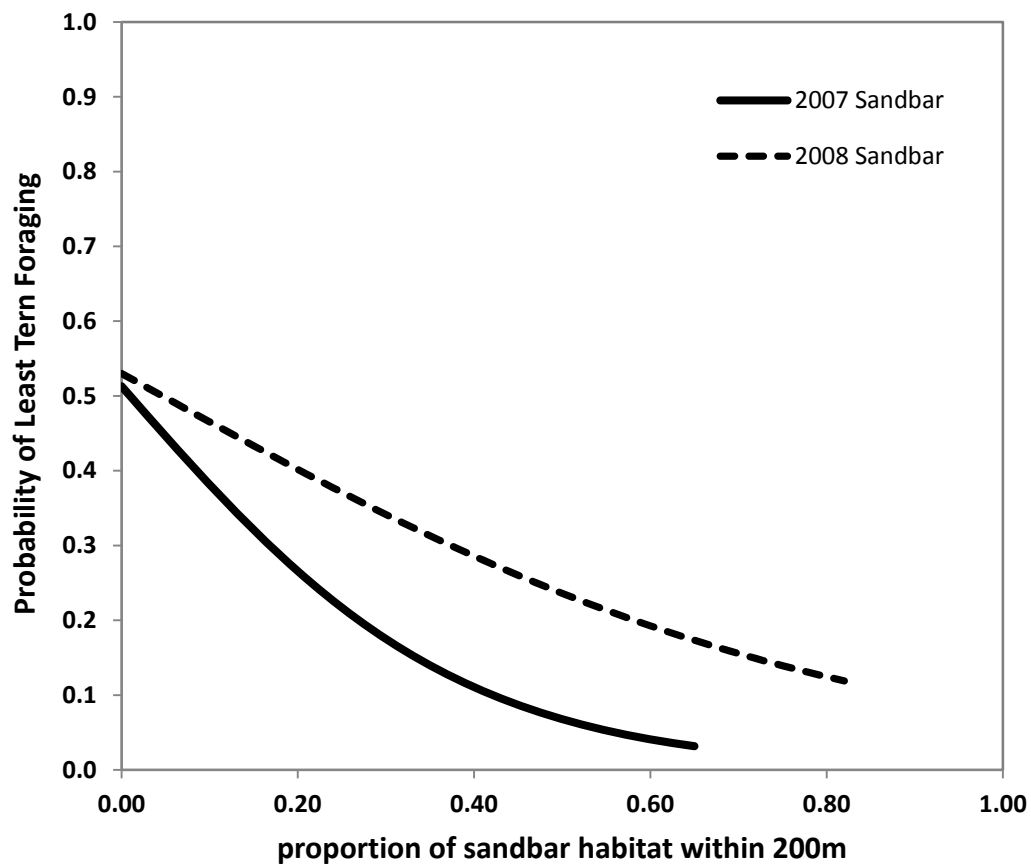


Figure 6. The proportion of sandbar within 200m and the probability of tern foraging as predicted by best model by year.

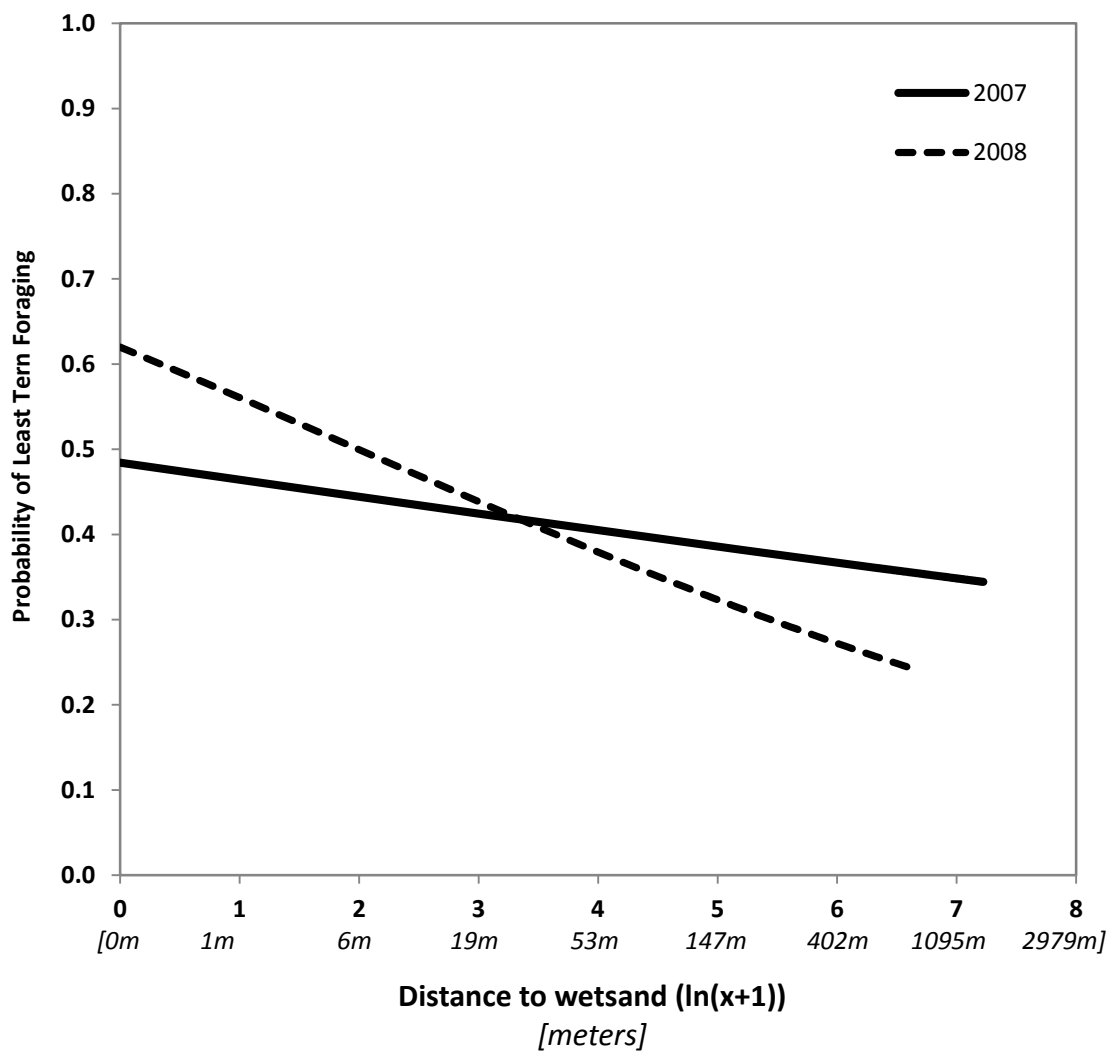


Figure 7. The proportion of wetsand habitat within 200m and the probability of tern foraging as predicted by best model by year.

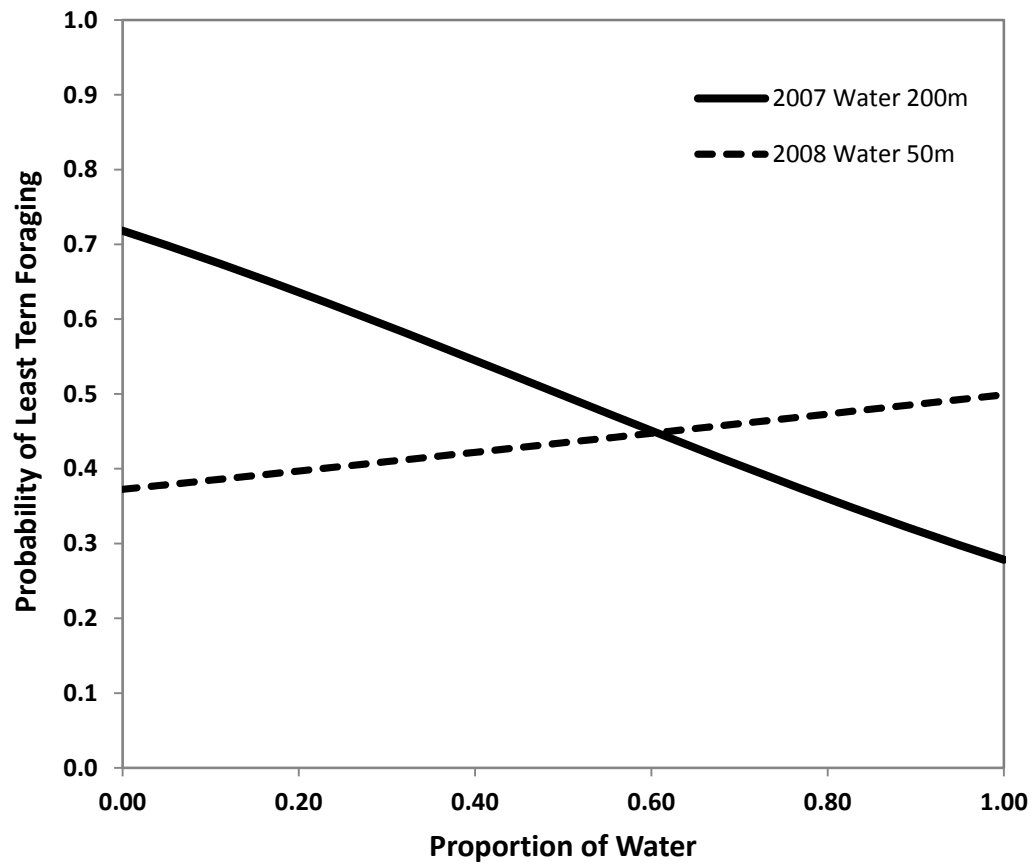


Figure 8. The proportion of water habitat (200m: 2007, 50m: 2008) and the probability of tern foraging as predicted by best fitting model.

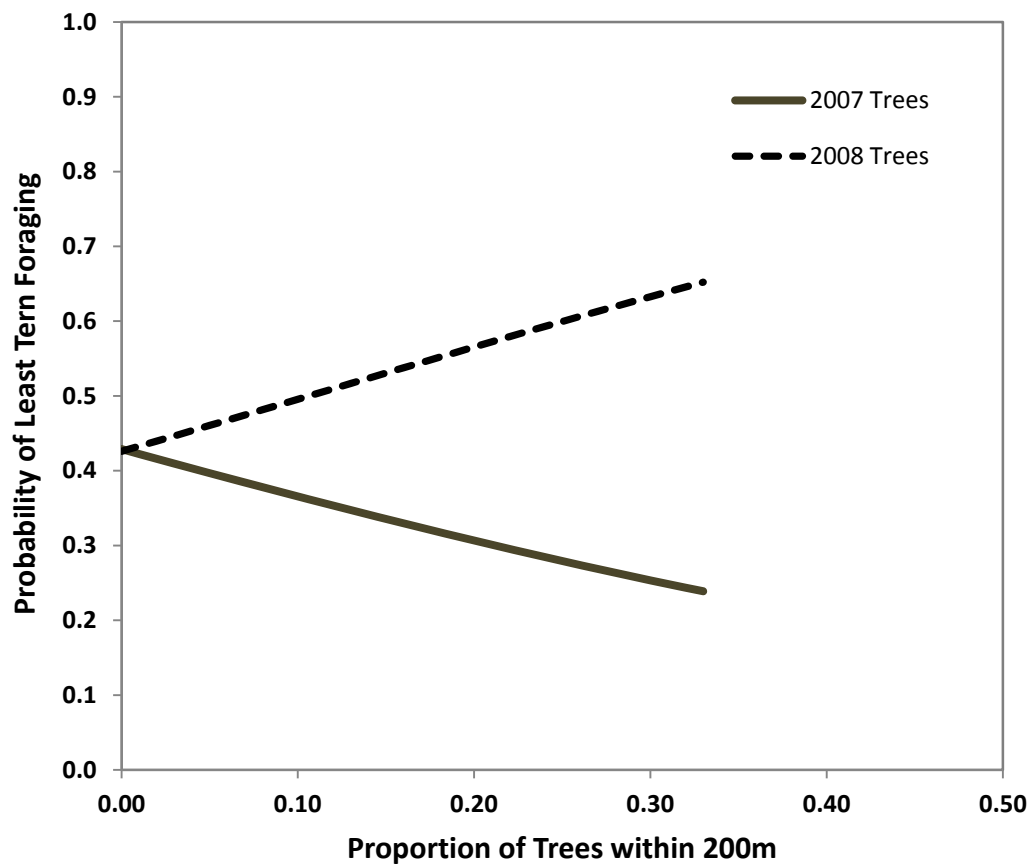


Figure 9. The proportion of tree habitat within 200m and the probability of tern foraging as predicted by best fitting model.

Chapter 4.

MANAGING THE HABITAT OR MANAGING THE CREATION PROCESS?

On the Missouri River, and throughout their range, Least Terns (*Sternula antillarum*) are dependent on habitats created by dynamic high-energy physical process. The barren coastlines and sandbars for nesting are generally free of vegetation due to deposition, erosion, and physical scour by wind, water and ice. The shallow water and shoals used for foraging Least Terns maintain their physical diversity, ecological productivity, and support of prey fish in large part due to river flows. When systems function in the way they were formed, the processes should maintain adequate habitat to support a stable population at the largest spatial scale. In reality, sandy rivers in the mid-continent, and world-wide, have now been dammed, many repeatedly. Consequently, the once historic movement of water, nutrients, debris and sediment through these river systems has fundamentally changed. Flood flow peaks are dampened and their phenology changed in favor of more gentle discharges, or discharges to meet other management objectives. Suspended sediment and river bed-load transport process are interrupted, trapped behind dams and within vast reservoirs. Sediment hungry rivers incise into their channel beds, reducing the likelihood of overbank flows and processes that lead to creation of complex shallow water environments in addition to emergent sandbars. Even if flows alone were used to maintain nesting habitats for Least Terns on the Missouri River, there is substantial

question about the ability of the system to maintain, in perpetuity, rates of deposition and erosion, which also sustain sandbars and shallow water habitat complexes.

Consequently, of what benefit are mechanical habitat creation and maintenance? I see them as neither good nor bad, but as a management practice, which relieves some of the symptoms of an impaired ecosystem. Construction of sandbars ensures that Least Terns continue to have habitat for nesting. But, nesting habitat management actions do not address the degradation of shallow water habitats used by Least Terns for foraging, or the fish that also depend on these habitats. Each major river within the interior basin struggles with the effects of dams, in combination with other river manipulations that change the timing and magnitude of flow and sediment, and therefore the ability of rivers to maintain their historic processes. Efforts to maintain some of these processes, and refine active habitat management appear crucial to perpetuating survival Least Terns within some of these modified environments.

As I wrote and revised these manuscripts, the 2011 record floods swept through the Missouri River basin reworking the research study area within which I worked. The magnitude of this record flood, a sustained 160,000 cfm in many areas for 4-6 weeks, was more than twice the discharge of the 1997 floods, and the largest flood since closure of the six Missouri River mainstem dams. Its influence on the system is predicted to provide substantial short-term ecosystem benefits for flood dependent species. And while there is excitement for evaluating a biological response to this flood phenomenon, there is also concern over some signs of further

system degradation. While researchers and managers strive to understand and describe the changes of this flood and management on the river and its effects on species, science plays an important role in elucidating those processes and relationships. Nevertheless, it is not science, but our society, its values, and economic and social constraints, which will make the decisions on the future of management of the Missouri River.

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