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Least Tern (*Sternula antillarum*) Population Response to Water Levels on Cheyenne River and Oahe Reservoir, South Dakota, USA

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Abstract.—Consideration of annual population count data, stream flows, water levels, and nesting habitat availability over a 29-year period suggest that Least Terns (*Sternula antillarum athalossos*) nesting along the Cheyenne River and Oahe Reservoir in South Dakota, USA, select areas primarily in response to reservoir water levels early in the breeding season. Generalized linear models were selected in an information-theoretic framework and showed important relationships between adult Least Tern numbers and reservoir levels, as well as a negative long-term temporal trend in both survey areas. Reservoir levels alone could not account for the temporal trend. The number of adult Least Terns on the Cheyenne River was positively correlated ($R = 0.668$) with mean May reservoir water levels—a more important relationship than that between adult numbers and river levels. The number of adults on the Oahe Reservoir was negatively correlated ($R = -0.573$) with mean May reservoir water levels. Numbers of adults on the Cheyenne River and on Oahe Reservoir were negatively correlated ($R = -0.684$), suggesting that birds may interact as one population across the two areas. This information should help managers to consider ecological relationships among segments of the Least Tern population on the Missouri River and its tributaries and options for managing Least Terns on the Cheyenne River, Oahe Reservoir, and elsewhere on the Missouri River system. Received 23 September 2016, accepted 12 January 2018.

Key words.—dispersal, ecology, Least Tern, population decline, reservoir, river, *Sternula antillarum athalossos*, water level.

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Development of large river systems for flood control and power generation can alter habitat and displace native species. The interior population of Least Terns (*Sternula antillarum athalossos*) was listed as federally endangered in the United States in 1985 due to population declines throughout its range (U.S. Fish and Wildlife Service 1985). In the upper Missouri River basin, Least Tern populations were impacted when natural sandbar nesting habitat and habitat connectivity were lost due to establishment of large dams and reservoirs. Interior Least Terns (hereafter, Least Terns) in the upper Missouri River population are described as having a segmental distribution (Lott *et al.* 2013). This consists of scattered colonies of Least Terns nesting on remnant sandbar habitat below some Missouri River dams, shoreline habitat along Missouri River reservoirs, and sandbar habitat on the Cheyenne River. These colonies are within the northernmost portion of the Least Tern range and are geographically isolated from other populations (Thompson *et al.* 1997).

Of these populations, the Cheyenne River and Oahe Reservoir Least Terns are nearest neighbors and are composed of small, scattered colonies nesting on river sandbars and reservoir shorelines. The extent to which individuals disperse between the two areas has not been evaluated, although fluctuations in adult numbers suggest considerable movement among breeding areas (Kirsch and Sidle 1999). Changes in numbers of adults among population segments when reservoir levels were high have been observed, but the relationships of these changes to water level variables has not been evaluated (U.S. Army Corps of Engineers 2014). Schwalbach (1988) documented nesting sites on the Missouri and Cheyenne Rivers in South Dakota and evaluated relationships of population numbers to local water levels within specific population segments but did not make comparisons among population segments in the river/reservoir system that might allow inference about dispersal or the impact of local water level changes on the broader population.

Reservoir levels and stream flows are primary factors affecting habitat availability for Least Terns during the nesting season. Shoreline habitat availability along the Oahe Reservoir is reduced when water levels are high and eliminated when water levels reach flood stage. Sandbar habitat availability on the Cheyenne River is affected by fluctuations in stream flows. While high flows in the spring are important for renewing suitable habitat conditions, high stream flows during the nesting season may inundate habitat, reduce or eliminate habitat availability, and cause mortality (Sidle *et al.* 1992).

We evaluated relationships between two populations of adult Least Terns and annual changes in stream flows on the Cheyenne River and water levels on the Oahe Reservoir over a 29-year period. We hypothesized that Least Terns in both locations were influenced by water level due to

its impact on nesting habitat. We also expected that the Cheyenne River population segment would show a decline over time, and that the decline might be related to fluctuations in water levels. Further, we hypothesized that changes in the small Cheyenne River population segment were influenced by dispersal from the larger Oahe Reservoir population segment, largely due to the impact of reservoir levels on nesting habitat availability on Oahe Reservoir. Due to the small size of the Cheyenne River population segment, we did not expect that the Oahe Reservoir population segment would be strongly influenced by dispersal from the Cheyenne River. While we were not able to estimate dispersal directly, we used comparisons among population changes and water level changes over time at both sites to make more limited inference about how the population segments interacted.

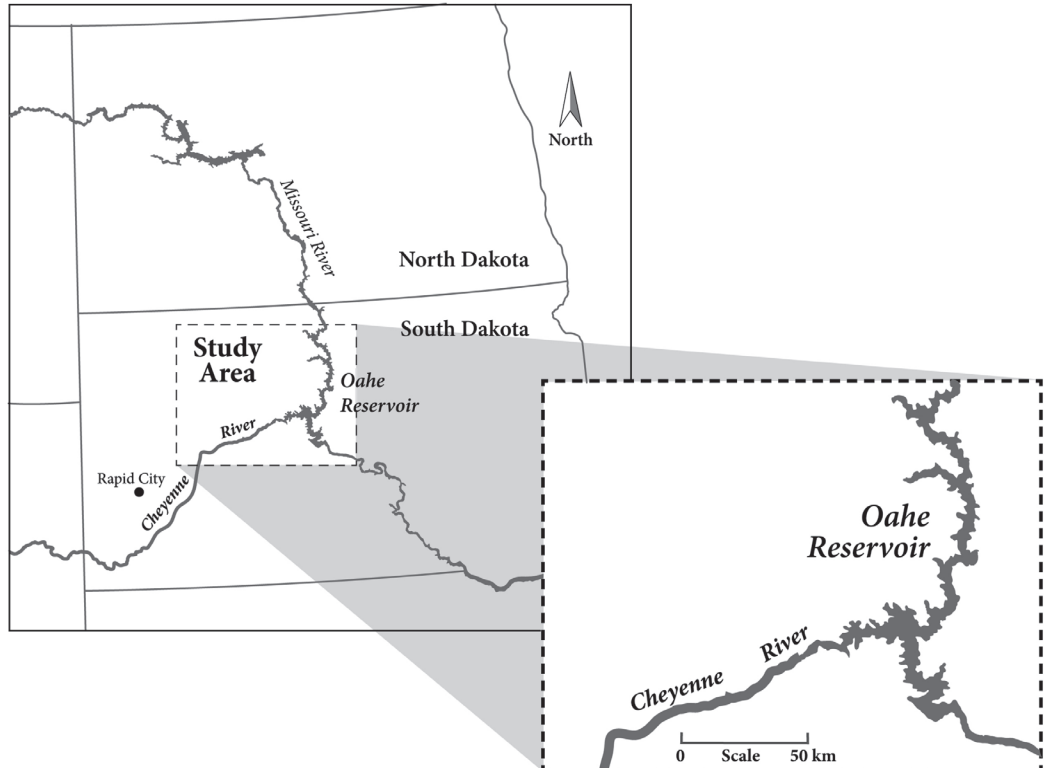


Figure 1. Study area in the lower Cheyenne River and Oahe Reservoir area of the Missouri River watershed, South Dakota, USA. Adult Least Tern survey results included coverage of the reservoir and river reach shown in the inset.

METHODS

Study Area

The Cheyenne River originates in the western Great Plains and flows into the Oahe Reservoir on the Missouri River in central South Dakota, USA (Fig. 1). Oahe Reservoir is a large impoundment of the Missouri River extending from central South Dakota into North Dakota. Stream flow rate on the Cheyenne River varies within and between years with weather and climate variability, as does water level on Oahe Reservoir; the reservoir's level is generally highest in the spring and gradually declines during the summer months. Small colonies of Least Terns have been documented nesting on sandbar habitat along a 90-km reach of the Cheyenne River and on shoreline areas along a 140-km reach of Oahe Reservoir since 1986 (Schwalbach 1988).

Survey Data

Systematic surveys were completed to document locations and numbers of nesting adult Least Terns in the upper Missouri River basin beginning in 1986, and have been conducted for monitoring the species' status since that time. Surveys were conducted every year on the Oahe Reservoir and 15 out of 30 years on the Cheyenne River, during the time period of 1986-2014. Survey data summarizing the number of adult Least Terns nesting along Oahe Reservoir shorelines from 1986 through 2014 were obtained from the U.S. Army Corps of Engineers (2014). Visual detection by a minimum of two observers was used to count all adults present during a single adult survey of Least Tern colony sites. The survey was scheduled after mid-June each year when the breeding season was under way to reduce potential effects of movement between areas. All beaches/sandbars were visually scanned from a boat or shoreline to determine presence of adults. If adults were observed, or the site was known to have adults nesting, a count would be conducted. All areas of potential habitat were surveyed. Protocols were implemented for duration, time of day, and avoiding surveys during inclement weather. Survey methods were described by U.S. Army Corps of Engineers (2009); limitations of the survey methods were discussed by Shaffer *et al.* (2013). Since the Cheyenne River sandbar and Oahe Reservoir shoreline colonies generally were composed of fewer adults, survey accuracy was likely higher on those sites than large sandbar colonies.

Stream Flow and Water Level Data

Daily stream flow data for the Cheyenne River and tributaries were used to calculate average and high flow levels, the number of peak flows, and the maximum peak flows for the months of May, June, and July for each year from 1986-2014 (U.S. Geological Survey 2015). Peak stream flows were defined as instances where daily flows exceeded 28.3 m³/sec on the Cheyenne River on any given day. This value was used to represent a stream flow that is high enough

to inundate sandbar nesting areas on the Cheyenne River. Average water level data for the Oahe Reservoir were obtained for May, June, and July, 1986-2014 (M. A. Swenson, pers. commun.). Oahe Reservoir is considered to be at flood stage (exclusive flood control level) when water reaches 492.9 m above mean sea level, which is the point at which nesting habitat is considered to be inundated.

Statistical Analysis

We used generalized linear models in an information-theoretic model selection framework (Burnham and Anderson 2002). To avoid undue model complexity, Pearson correlation coefficients were used to initially develop a subset of candidate water variables that did not have high collinearity ($R < 0.6$; Dormann *et al.* 2013) and that would be most useful in modeling. For candidate variables in model selection, we used the single Cheyenne River stream flow variable and the single Oahe Reservoir water level variable with the strongest correlations to the population count data. To test hypotheses regarding trend over time, year was included as an independent variable. We also included the number of Oahe Reservoir Least Tern adults as a variable in the Cheyenne River Least Tern models to test the hypothesis that the Cheyenne River population segment was influenced by dispersal from the Oahe Reservoir population segment.

Consequently, 12 models were developed for Cheyenne River Least Terns based on the *a priori* hypotheses about the relationship of population variability over time to water variables and to the Oahe population segment (Table 2). The models included four one-variable models, five two-variable models, two three-variable models, and the null (intercept only) model. Four models were developed for the Oahe Reservoir Least Terns incorporating reservoir level and year, including two one-variable models, one two-variable model, and the null model. No interaction terms were included in any model.

For each set of models, the Akaike's information criterion for small samples (AIC_c) and Akaike weights (w_i) were computed, and parameter estimates, standard errors, and 95% confidence intervals obtained for individual models using PROC GLIMMIX (SAS Institute, Inc. 2011). Models were then ranked based on the AIC_c , separately for the two populations. The number of observations (years) for the models for Cheyenne River and Oahe Reservoir Least Terns were 15 and 29, respectively. Since the dependent data were integer counts (number of adults) where the variance far exceeded the mean, the negative binomial distribution was used for the underlying model. Generalized linear model diagnostics included plots of predicted vs. observed, residual vs. predicted, and residual vs. all independent variables. Because observations were multi-annual time series, autocorrelation functions were used to examine model residuals for temporal autocorrelation to address any possible violation of the among-years independence assumptions implicit in the models (Venables and Ripley 2002).

Cheyenne River Habitat Analysis

While it did not constitute a formal component of our analysis of population change over time, we were interested in evaluating whether the gross quantity of sandbar habitat on the Cheyenne River had changed over the study period. The intent was not to evaluate inter-annual habitat change in relation to population numbers, but rather to rule out gross loss or gain of nesting habitat (due to channelization, for instance) as a factor affecting Least Tern numbers on the Cheyenne River over the long term. Change in sandbar habitat quantity on the Cheyenne River was evaluated by comparing Landsat Thematic Mapper satellite imagery for two dates corresponding to the beginning and end years of the study period: 17 July 1984 and 28 July 2011. These were considered the best images available with minimal cloud cover and similar stream flow rates, 22.8 m³/sec and 24.1 m³/sec, respectively.

ArcGIS software was used to composite individual image raster bands into multiple layer stack files, and then the Iso Cluster program was used to produce a set of 60 unique spectral signatures per image date (Environmental Systems Research Institute 2011). A maximum likelihood unsupervised classification routine was used along with manual image interpretation to label classes into categories of sandbar, water, or non-habitat. The difference in sandbar habitat between the two dates provided an estimate of change between 1984 and 2011.

RESULTS

Mean monthly reservoir water levels were 488.0, 488.4, and 488.3 m above mean sea level for May, June, and July, respectively, during the period 1986-2014. Mean monthly reservoir water levels were above flood stage two years in May, six years in June, and six years in July. Mean reservoir levels were low throughout the May-July season for 17 years during the period. Mean monthly stream flows on the Cheyenne River were 67.1, 57.6, and 21.8 m³/sec for May, June, and July, respectively. Maximum stream flows were 311.8, 216.3, and 59.6 m³/sec for May, June, and July. The maximum number of days with peak stream flows was 31, 30, and 26 during May, June, and July, respectively. The mean number of days with peak stream flows was 13, 12, and 6 for May, June, and July, respectively. There were three years during the study period when no peak flows occurred in May, June and July: 2002, 2006 and 2012.

The number of adult Least Terns on the Cheyenne River ranged from a high of 60 in

1986 to a low of four in 2013. The number on Oahe Reservoir ranged from a high of 192 in 1991 to 30 in 1987. Cheyenne River Least Tern numbers were inversely correlated to Oahe Reservoir Least Tern numbers over time ($R = -0.684$; Fig. 2). In the preliminary correlation screening, Cheyenne River Least Tern numbers showed a positive correlation with reservoir water levels and stream flows, whereas Oahe Reservoir Least Tern numbers showed an inverse correlation with reservoir water levels and stream flows (Table 1). The mean reservoir water level in May was the strongest predictor of both the Cheyenne River and Oahe Reservoir Least Tern numbers (Table 1; Fig. 3). These relationships were next explored through model selection.

Of the 12 models evaluated for Cheyenne River Least Terns, the lowest ΔAIC_c model was a function of Oahe Reservoir water level in May and year (Table 2). Based on the parameters of this model, adult Least Tern numbers on the Cheyenne River were higher when reservoir levels were high, but also decreased over time since 1986 regardless of reservoir level (Table 3). There were two top models for Oahe Reservoir Least Terns, within

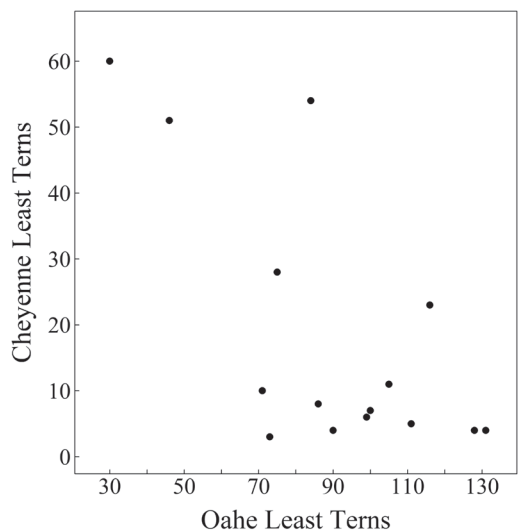


Figure 2. Cheyenne River and Oahe Reservoir adult Least Tern numbers in relation to one another. $n = 15$ years available for comparison. Pearson Correlation coefficient = -0.684 .

Table 1. Pearson correlations for Cheyenne River and Oahe Reservoir adult Least Tern numbers and water variables.

Variable	Cheyenne River Adult Least Terns <i>n</i> = 15 years		Oahe Reservoir Adult Least Terns <i>n</i> = 29 years	
	Correlation	<i>P</i> -value	Correlation	<i>P</i> -value
May River Mean	0.578	0.024	-0.476	0.009
May River Maximum	0.437	0.104	-0.433	0.019
May River Peaks	0.382	0.160	-0.438	0.018
May Reservoir Mean	0.668	0.007	-0.573	0.001
June Reservoir Mean	0.657	0.008	-0.551	0.002
July Reservoir Mean	0.641	0.010	-0.526	0.003
May-June-July Reservoir Mean	0.659	0.008	-0.553	0.002
June-July Reservoir Mean	0.649	0.008	-0.539	0.003

two ΔAIC_c units and with similar Akaike weights (Table 2). A one-variable model included reservoir water level in May, with an inverse relationship to Oahe Reservoir Least Tern numbers, and a two-variable model included year, indicating decline over time (Table 3). However, the 95% confidence interval on the year parameter estimate included zero, suggesting high uncertainty in the trend estimate. All 12 models are included in Table 2 for comparison purposes (Burnham *et al.* 2011).

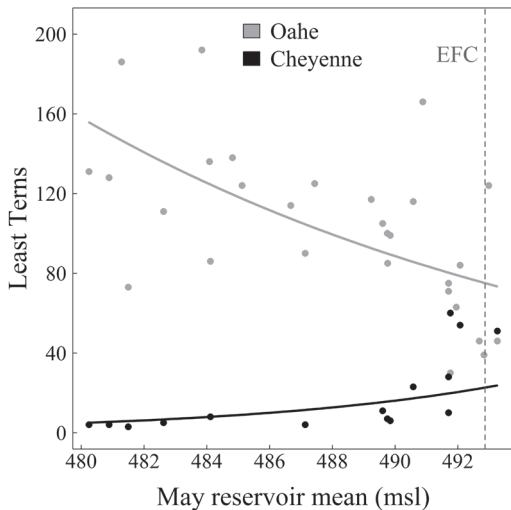


Figure 3. Cheyenne River and Oahe Reservoir adult Least Tern numbers in relation to mean Oahe Reservoir water level in May. Solid lines show the estimated effect of reservoir level on adult Least Tern numbers, controlling for a year effect, in the highest-supported models. EFC = Exclusive Flood Control level, which corresponds to flood stage on Oahe Reservoir; msl = mean sea level.

It appeared that with higher reservoir water levels in the early part of the breeding season, the Cheyenne Least Tern population segment increased, whereas the Oahe population segment decreased. Oahe Least Tern numbers were at their highest when reservoir levels were low and lowest when reservoir levels reached flood stage, as expected if flooding eliminates nest site availability (Figs. 3 and 4). In addition, both population segments showed some evidence of decline over time, an effect for which water levels did not account (Fig. 4). Autocorrelation functions identified no temporal autocorrelation in model residuals (95% confidence intervals) for the top models, suggesting that once the relationships with reservoir water level and year had been accounted for there was no temporal dependence in the remaining year-to-year unexplained variability.

Comparison of classified satellite imagery showed an increase in sandbar habitat on the Cheyenne River at comparable stream flow levels between 1984 and 2011 (Table 4). Thus, although we did not quantify inter-annual variability, there was no indication that gross loss of suitable nesting habitat occurred during this time frame.

DISCUSSION

Our results show important relationships among Cheyenne River Least Terns, Oahe Reservoir Least Terns, and Oahe Reservoir water levels. Across a 29-year pe-

Table 2. Generalized linear models for Cheyenne River and Oahe Reservoir adult Least Tern counts in relation to water variables and year, ranked based on Akaike's information criterion for small samples (AIC_c), the change in AIC_c (ΔAIC_c), and Akaike weight (w_i). Models with lower ΔAIC_c and higher w_i have more support. K is the number of model parameters.

Variables	$-2\text{Log}_e(L)$	K	AIC_c	ΔAIC_c	w_i
Cheyenne River Least Tern Models					
May Reservoir Mean, Year	85.52	3	97.52	0.000	0.814
Oahe Adults, May Reservoir Mean, Year	85.43	4	102.09	4.569	0.083
May River Mean, Year	90.64	3	102.64	5.112	0.063
Year	96.43	2	104.61	7.083	0.024
Oahe Adults, May River Mean, Year	90.13	4	106.80	9.275	0.008
Oahe Adults, Year	95.98	3	107.98	10.461	0.004
May Reservoir Mean	100.73	2	108.91	11.385	0.003
Oahe Adults, May Reservoir Mean	98.49	3	110.49	12.970	0.001
Oahe Adults, May River Mean	104.10	3	116.10	18.577	0.000
Oahe Adults	109.52	2	117.71	20.182	0.000
May River Mean	112.51	2	120.69	23.167	0.000
Null	118.27	1	123.27	25.748	0.000
Oahe Reservoir Least Tern Models					
May Reservoir Mean	286.01	2	292.97	0.000	0.534
May Reservoir Mean, Year	283.64	3	293.31	0.340	0.451
Null	296.32	1	300.79	7.818	0.011
Year	295.46	2	302.42	9.454	0.005

riod, in years when reservoir water level was low during the early breeding season, Least Tern numbers on the Oahe Reservoir were high but numbers on the Cheyenne River were low, and the opposite was true in years when reservoir water level was high. Reservoir water level was more strongly correlated with Cheyenne River Least Tern numbers than were the river stream flow variables, but the relationships were broadly similar (Table 1). This is counterintuitive in terms of beach and sandbar habitat avail-

ability, but can potentially be explained by dispersal dynamics, in light of the inverse relationship between population numbers at the two study sites.

Least Terns are known to move from one breeding area to another depending on habitat availability, and it has been speculated that they disperse more from less stable nesting sites (Boyd and Thompson 1993; Thompson *et al.* 1997). The relationship we found between the small Cheyenne River population segment and the comparatively

Table 3. Parameter estimates for the lowest AIC_c models for Cheyenne River adult Least Terns (one model) and Oahe Reservoir adult Least Terns (two models), with standard errors and confidence intervals. Key variables included mean reservoir water level in May and year.

Variable	Parameter Estimate	Standard Error	95% Confidence Interval
Cheyenne Least Tern Model			
Intercept	-54.341	16.462	-90.209, -18.472
May Reservoir Mean	0.119	0.033	0.046, 0.192
Year	-0.075	0.015	-0.109, -0.042
Oahe Least Tern One-variable Model			
Intercept	31.6848	7.8028	15.6747, 47.6949
May Reservoir Mean	-0.0555	0.0160	-0.0883, -0.0227
Oahe Least Tern Two-variable Model			
Intercept	32.958	7.483	17.577, 48.340
May Reservoir Mean	-0.058	0.015	-0.089, -0.026
Year	-0.012	0.008	-0.028, 0.004

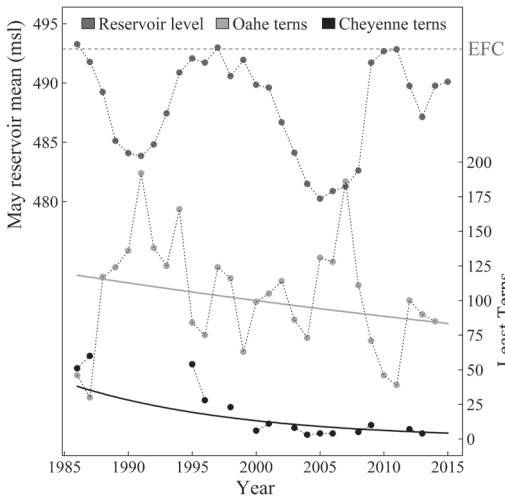


Figure 4. Cheyenne River and Oahe Reservoir adult Least Tern numbers in relation to year and mean Oahe Reservoir water levels in May. Both Least Tern population segments showed a decline over time. Solid lines show the estimated effect of year on adult Least Tern numbers, controlling for the effect of reservoir level, in the highest-supported models. EFC = Exclusive Flood Control level, which corresponds to flood stage on Oahe Reservoir; msl = mean sea level.

larger Oahe Reservoir population segment suggests that the birds interact across the two areas as part of a single population, consistent with regional population designations (Lott *et al.* 2013). The finding that Oahe Reservoir water levels are the predominant variable affecting adult numbers in both areas suggests that the Cheyenne River may serve as a ‘spillover’ area, with birds moving up the Cheyenne River in years when reservoir water levels are high and habitat availability low, forcing Oahe birds to find habitat up-river on the Cheyenne or elsewhere on the Missouri River system. More intensive efforts such as banding or radio-telemetry would be needed to confirm movement between these areas.

This dynamic can explain much of the inter-annual fluctuation in adult numbers, but it does not explain the gradual long-term decline in both areas over the study period (Fig. 4). It is not known whether this decline has been driven by emigration to more suitable colony sites elsewhere on the Missouri River system. Least Terns are known to have high site fidelity in some breeding areas (Burger 1984; Atwood and Massey 1988; Renken and Smith 1995a) and high adult survival rates (Renken and Smith 1995b). It is possible that a component of the breeding population has high site fidelity and continued to return to nest on the Cheyenne River and Oahe Reservoir over many years, but with poor reproductive success, resulting in the long term decline.

Sandbar habitat quantity on the Cheyenne River was greater in 2011 than 1984, suggesting that this was not a limiting factor for Least Tern nesting. However, habitat availability during the nesting season is affected by fluctuations in stream flows in relation to sandbar elevation, which our image analysis was not able to quantify (Lott *et al.* 2013). While the frequency of high flows could cause direct impacts on Least Tern nesting success, including inundation and loss of nests, this was not found to be an important factor related to inter-annual variability in the number of adults on the Cheyenne River. Over the long term, stream flow characteristics on rivers such as the Cheyenne may be affected by broad scale changes in precipitation across the Great Plains including the Missouri River and its major tributaries (Norton *et al.* 2014). These changes are consistent with findings of increases in spring, summer, and autumn precipitation from 1970 to 2005 across the Upper Midwestern region (Pryor *et al.* 2009). Further increases in heavy precipitation events are expected in

Table 4. Change in the amount of sandbar habitat (ha) on the Cheyenne River, comparing Landsat satellite images from 17 July 1984 and 28 July 2011. These were considered the best images available with minimal cloud cover and similar stream flow rates, 22.8 m³/sec and 24.1 m³/sec, respectively, during the time period included in the study.

Category	1984	2011	Change
Sandbar habitat	365.74	1,056.34	+690.60
Water	1,453.08	1,194.56	+146.16
Non-habitat	24,353.44	23,516.66	-836.79
Total ha	26,172.25	26,172.25	

the Northern Hemisphere in coming decades (Intergovernmental Panel on Climate Change 2013; Fischer and Knutti 2015). Increases in the average or frequency of peak stream flows on the Cheyenne River combined with high water levels on the Oahe Reservoir during the May-July nesting season may continue to affect the Least Tern population in both areas.

The declining trend for both Cheyenne River and Oahe Reservoir Least Terns may be related to low productivity, low return rates, low immigration rates, or some combination of these; however, our ability to make demographic inferences from annual surveys of unmarked adults is very limited. Nonetheless, the availability of suitable nesting habitat on the Cheyenne River and Oahe Reservoir through periods of high and low water levels is likely to influence whether Least Terns persist in the area. Evaluating the response of Least Tern populations to changes in reservoir water levels and stream flows across areas and over time, particularly in combination with monitoring of marked birds and nests, can improve understanding of population dynamics for the species. This study may help managers consider ecological relationships among segments of the Least Tern population on the Missouri River and its tributaries and options for managing Cheyenne River and Oahe Reservoir Least Terns.

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